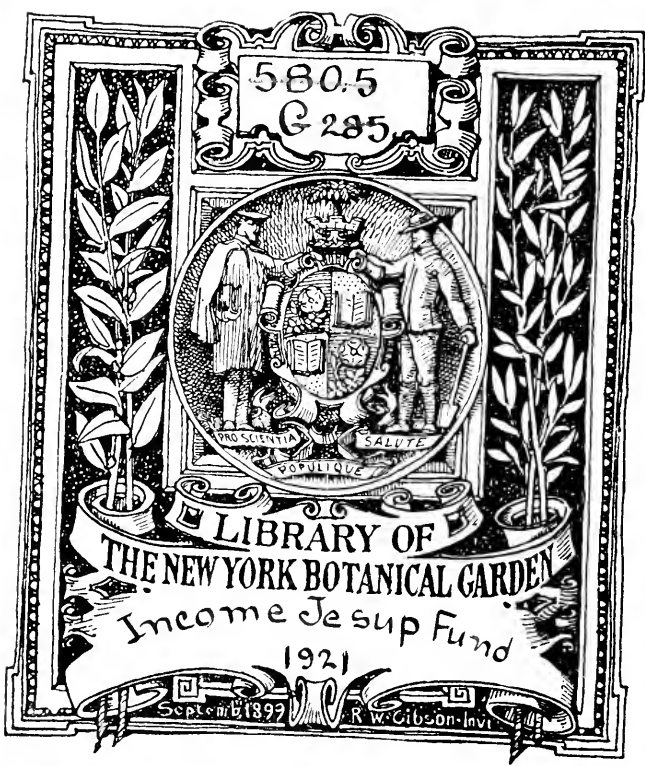


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JOURNAL OF GENETICS

EDITED BY

W. BATESON, M.A., F.R.S.

DIRECTOR OF THE JOHN INNES HORTICULTURAL INSTITUTION

AND

R. C. PUNNETT, M.A., F.R.S.

ARTHUR BALFOUR PROFESSOR OF GENETICS IN THE UNIVERSITY OF CAMBRIDGE

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STUDIES OF INHERITANCE IN THE JAPANESE CONVOLVULUS. PART II.

By B. MIYAZAWA.

(With One Coloured Plate.)

INTRODUCTION.

SINCE the culture experiments ending with 1918 have led me to certain definite conclusions in respect to the hereditary behaviour of various shades of flower-colours which appear in the F_2 generation, and which were shortly noticed in my previous paper¹, I should like to describe below the results of these experiments. In my previous article I have mentioned the fact that yellow plants never bear dark-red flowers, but recently I was able to get a yellow-leaved race which nevertheless produces dark-red flowers; and as I have conducted hybridisation experiments between such a race and each of the two original parents, the results so far obtained will be given also in this paper.

First of all, I will mention here briefly some results obtained by many investigators as regards the inheritance of flower-colours which seem to have special relations with my own studies.

Bateson and Punnett² reported in *Lathyrus odoratus* several cases where the flower-colour presented by neither parent appears in F_1 or in and after F_2 . Saunders³ found in *Matthiola* that certain two white-flowered individuals crossed together gave coloured F_1 , and such a case was also reported by Marryat⁴ and by Takezaki⁵ in *Mirabilis* and Japanese *Convolvulus*, respectively. Saunders⁶ obtained purple-flowered F_1 between pink and white varieties of *Salvia Horminum*, and in F_2 the ratio was

¹ *Journal of Genetics*, Vol. VIII. No. 1, p. 62, 1918.

² *Reports to the Evolution Committee of the Royal Society*. II. pp. 83—99, 1905.

³ *L.c.* I. p. 45.

⁴ *L.c.* V. p. 46.

⁵ "Nippon Ikusyugakukai Kwaihō" (*Journal of the Japanese Breeders' Association*), I. 1, Tab. V and VI. 1916.

⁶ *Reports to the Evolution Committee of the Royal Society*, 1905. II. p. 50.

2 Inheritance in the Japanese *Convolvulus*. Part II

9 purple : 3 pink : 4 white. Tschermak¹ also got similar results in *Pisum sativum*. All these cases shew that the cooperation of the two factors is necessary for the production of anthocyanin.

The fact that the diluting or modifying factor is present in the flower of *Matthiola* was confirmed by Saunders²; Bateson and Punnett³ also reported a case in *Lathyrus* that can be explained by the presence of the diluting factor.

Baur⁴ found in *Antirrhinum* that zygotes heterozygous for **L** in the presence of **D** are pale magenta in flower-colour, whereas those homozygous for **L** are intermediate magenta in the same respect. Marryat⁵ discovered in *Mirabilis* the occurrence of heterozygous forms with flower colours which may be best represented by the following formulae :

CCMM.....	crimson
CcMM	magenta
CcMm	magenta rose
CCMm	orange red
CCmm	yellow
Ccmm	pale yellow

A case where the effects of the one factor, **T**, are not manifested unless the other, **L**, is at the same time present in the zygote was studied by Wheldale⁶ in *Antirrhinum*; namely, no magenta colour appears in the flower tube unless there is magenta colour in its lips.

Bateson⁷ studied the relation between the colour and the shape of flower in *Lathyrus*, and found that in that having the hooded standard the colours of the standard and wings agree with each other, but in that having the erect-standard they do not.

EXPERIMENTS.

I. F_2 GENERATION.

As the characters of both parents as well as the F_1 plant are already described in Part I⁸ of this paper I will not repeat them here, but as to the flower-colour of each F_2 plant, though it was described in the

¹ *Zeitschrift für induktive Abstammungs und Vererbungslehre*, 1912, Bd. vii. pp. 81—234.

² *Proceedings of the Royal Society*, Vol. LXXVII. 1905, pp. 236—238.

³ *Reports to the Evolution Committee of the Royal Society*, 1906. III. p. 33.

⁴ *Zeitschrift für induktive Abstammungs und Vererbungslehre*, 1910, Bd. iii. pp. 34—98.

⁵ *Reports to the Evolution Committee of the Royal Society*, 1909. V. pp. 42—46.

⁶ *Proceedings of Royal Society of London*, 1907, Vol. LXXIX. B, pp. 288—305.

⁷ *Journal of Genetics*, Vol. VIII. No. 1, pp. 61, 62.

⁸ *L.c.* pp. 61, 62.

previous paper¹, I should like to repeat it here shortly. In F_2 not only do we find flowers of white, dark-red and magenta colour, exactly similar to those of the two original parents and the F_1 plant, respectively, but also we have those of scarlet colour; and besides, in each of these colours—dark-red, magenta, and scarlet—there are three gradations of tone, sharply distinguishable from each other, which I will call *light*, *medium* and *deep*, respectively. (See Pl. I, figs. 1—9.)

The details of the segregation of leaf- and flower-colours in F_2 are shewn in Table I.

TABLE I.

Leaf-colour	Flower-colour	Actual numbers of individuals	Expected
Green	light magenta ...	164	166.500
	magenta ...	74	83.250
	deep magenta ...	72	83.250
	light scarlet ...	48	55.500
	scarlet ...	24	27.750
	deep scarlet ...	24	27.750
	light dark-red ...	111	111.000
	dark-red ...	69	55.500
	deep dark-red ...	58	55.500
	white ...	217	222.000
Yellow	light magenta ...	95	83.250
	magenta ...	45	41.625
	deep magenta ...	49	41.625
	light scarlet ...	32	27.750
	scarlet ...	14	13.875
	deep scarlet ...	14	13.875
	light dark-red ...	0	—
	dark-red ...	0	—
	deep dark-red ...	0	—
	white ...	74	74.000
Totals ...		1184	

Here it may be remarked that in the above Table the results of two reciprocal crosses as well as those of the F_2 experiments repeated in 1917 are all summed up, because I have found no essential difference among all these results.

In Table I we see that in green plants the ratio between magenta, scarlet, and dark-red is nearly equal to 3:1:2, and that in yellow plants that between magenta and scarlet is nearly equal to 3:1, and moreover, it will be seen that of the three gradations of the tone of each colour the ratio of light:medium:deep is 2:1:1. In order to explain such results I have adopted the following genetic formulae for the two parents:

$$A = ggddBBMM,$$

$$B = GGDDbbmm.$$

¹ *L.c.* p. 62.

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The meaning of the factors is as follows :

G, the factor for green colour in the leaf.

D, that for dark-red flower-colour when the accompanying **G** is in homozygous condition ; it produces, however, scarlet colour when **G** is present as **Gg**, or when it is altogether absent (i.e. **gg**) and **B** is also absent.

B, that for blue colour ; in the presence of **D** its effects are not manifest when **G** is present as **GG** ; it produces magenta colour both in homo- and heterozygous condition, when **G** is in the condition **Gg** or **gg**.

M, that for modifying the tone of flower-colour both in homo- and heterozygous condition, i.e. the *medium* grade of magenta, scarlet, or dark-red colour is produced when **M** is present and the plant is also homozygous for **D** ; the *light* grade of each of these colours is produced when **M** is present and the plant is at the same time heterozygous for **D** ; and finally the *deep* grade appears when **M** is altogether absent.

The genetic constitution of each F_1 plant is naturally **GgDdBbMm**, and when it is self-fertilised we expect 81 zygotes of different genetic constitutions, as is shewn in Table II. Thus we may acknowledge that my hypotheses above stated will well explain all my results. It is necessary to add here that though the meaning of the factor **D** is somewhat more broadened in this than in my first paper, inasmuch as not only is its action intimately bound with **G** but also with **B**, nevertheless my view in respect to the relation between green leaf and dark-red flower-colour remains quite unchanged.

II. BACK-CROSSING.

In 1916 the back-crossing of one F_1 plant by both of the two parents, *A* or *B* was done.

1. $F_1 \times A$ (= **GgDdBbMm** \times **ggddBBMM**).

The results are shewn in Table III.

TABLE III.

		Light magenta	White	Totals
Green	...	33	48	81
Yellow	...	45	38	83
Totals	...	78	86	164
Expected	...	$\left. \begin{array}{l} 41 \\ 41 \end{array} \right\}$	$\left. \begin{array}{l} 41 \\ 41 \end{array} \right\}$	

In this case, as was described in my previous paper, it will be seen that the ratios between green and yellow plants and between light magenta and white are 1 : 1, respectively ; and besides, coloured flowers

TABLE II.

Genetic constitutions	Number of individuals	Flower colour	Leaf colour	Genetic constitutions	Number of individuals	Flower colour	Leaf colour
GgDdBBMM	(4)	Light magenta	Green	ggDdBBMM	(2)	Light magenta	Yellow
GgDdBBMm	(8)			ggDdBBMm	(4)		
GgDdBbMM	(8)			ggDdBbMM	(4)		
GgDdBbMm	(16)			ggDdBbMm	(8)		
GgDDBBMM	(2)	Magenta		ggDDBBMM	(1)	Magenta	
GgDDBbMM	(4)			ggDDBbMM	(2)		
GgDDBBmM	(4)			ggDDBBmM	(2)		
GgDDBbMm	(8)			ggDDBbMm	(4)		
GgDDBBmm	(2)	Deep magenta		ggDDBBmm	(1)	Deep magenta	
GgDDBbmm	(4)			ggDDBbmm	(2)		
GgDdBbmm	(4)			ggDdBbmm	(2)		
GgDdbbmm	(8)			ggDdbbmm	(4)		
GgDdbbMM	(4)	Light scarlet		ggDdbbMM	(2)	Light scarlet	
GgDdbbMm	(8)			ggDdbbMm	(4)		
GgDDBbMM	(2)	Scarlet		ggDDBbMM	(1)	Scarlet	
GgDDBbMm	(4)			ggDDBbMm	(2)		
GgDDBbmm	(2)	Deep scarlet		ggDDBbmm	(1)	Deep scarlet	
GgDdbbmm	(4)			ggDdbbmm	(2)		
GGDdBbMM	(4)	Light dark-red		ggddBBMM	(1)	White	
GGDdBBMm	(4)			ggddBbMM	(2)		
GGDdBbMm	(8)			ggddBBMm	(2)		
GGDdbbMM	(2)			ggddBBmm	(1)		
GGDdBBMM	(2)			ggddbbMM	(1)		
GGDdbbMm	(4)			ggddBbMm	(4)		
GGDDBBMM	(1)	Dark-red		ggddBbmm	(2)		
GGDDBbMM	(2)			ggddbbmM	(2)		
GGDDBBmM	(2)			ggddbbmm	(1)		
GGDDBbMm	(1)						
GGDDBbMm	(4)						
GGDDBbMm	(2)						
GGDDBBmm	(1)	Deep dark-red					
GGDDBbmm	(1)						
GGDDBbmm	(2)						
GGDdBBmm	(2)						
GGDdbbmm	(2)						
GGDdBbmm	(4)						
GGddBBMM	(1)	White					
GGddbbMM	(1)						
GGddBBmM	(1)						
GGddBbMM	(2)						
GGddBBMm	(2)						
GGddBbMm	(4)						
GGddBbmm	(2)						
GGddbbmM	(2)						
GGddbbmm	(1)						
GgddBBMM	(2)						
GgddBBMm	(4)						
GgddBbMM	(4)						
GgddBBmm	(2)						
GgddbbMM	(2)						
GgddBbMm	(8)						
GgddBbmm	(4)						
GgddbbMm	(4)						
Ggddbbmm	(2)						

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are light magenta exclusively. The reason for this will readily be seen when we compare the genetic constitutions of the F_1 and A plants.

2. $F_1 \times B$ (= GgDdBbMm \times GGDDbbmm).

The results are shewn in Table IV.

TABLE IV.

	Light magenta	Magenta	Deep magenta	Light scarlet	Scarlet	Deep scarlet	Light dark- red	Dark- red	Deep dark- red	White	Totals
Green	8	6	12	4	7	9	9	11	15	0	81
Yellow	0	0	0	0	0	0	0	0	0	0	0
Expected	{ 5·063 0	{ 5·063 0	{ 10·125 0	{ 5·063 0	{ 5·063 0	{ 10·125 0	{ 10·125 0	{ 10·125 0	{ 20·250 0	{ 0 0	

In this case all plants have green leaves and we find magenta, scarlet, and dark-red flowers in all their respective three tones. If we add together individuals of each colour belonging to the same tone it will be seen that the ratio magenta:scarlet:dark-red is 1:1:2, and in each colour there are two plants of deep tone for each one of the two other tones. Here again the facts are clearly in accordance with hypotheses put forward.

III. F_3 , F_4 , AND F_5 GENERATIONS, ETC.

I have made a series of breeding experiments on various families in F_3 , F_4 , and F_5 ; moreover, various crosses were made among the offspring of the hybrids both with one another and with the original parents, the offspring in each case being grown on. All these experiments have fully borne out my interpretation above given, and since I have never encountered any contradictory case, I will not describe here details of all these results, but simply some few selected examples.

1. *Green plant with magenta flower.*

The results are shewn in Table V.

TABLE V.

		Magenta	Scarlet	Dark-red	Totals
F_3 , No. 31	{ green	40	8	32	80
	{ yellow	12	7	0	19
F_4 , No. 31—1	{ green	22	7	14	43
	{ yellow	13	2	0	15
Totals	{ green	62	15	46	123
	{ yellow	25	9	0	34
Expected	...	{ 58·875	19·625	39·250	
		{ 29·437	9·813	0	

It is apparent from the above Table that in green plants the ratio magenta:scarlet:dark-red is 6:2:4, and that in yellow plants the ratio magenta:scarlet is 3:1, so that we must consider that the genetic constitution of the plant used is **GgDDBbMM**.

2. *Green plant with deep magenta flower.*

The results are indicated in Table VI.

TABLE VI.

		Deep magenta	Deep dark-red	Totals
No. 9—23	{ green	51	23	74
	{ yellow	21	0	21
95				
Expected	{ green	47.50	23.75	
	{ yellow	23.75	0	

It will be seen from the above Table that the ratio green, deep magenta: green, deep dark-red: yellow, deep magenta is 2:1:1. Thus we may consider the genetic constitution of the plant used to have been **GgDDBBmm**.

3. *Green plant with light scarlet flower.*

The results are as follows:

TABLE VII.

	Light scarlet	Scarlet	Deep scarlet	Light dark-red	Dark-red	Deep dark-red	White	Totals
No. 60	{ green	20	10	11	7	6	4	20
	{ yellow	7	4	4	0	0	0	78
101								
Expected	{ 18.938	9.469	9.469	9.469	4.734	4.734	18.938	
	{ 9.469	4.734	4.734	0	0	0	6.313	

From the above Table we see that in green plants light scarlet:scarlet:deep scarlet:light dark-red:dark-red:deep dark-red:white are in the ratio 12:6:6:6:3:3:12, and in yellow plants light scarlet:scarlet:deep scarlet:white are in the ratio 6:3:3:4. Thus the genetic constitution of the plant used must have been **GgDdbbMm**.

4. *Green plant with scarlet flower.*

The results are shewn in Table VIII.

TABLE VIII.

		Scarlet	Deep scarlet	Dark-red	Deep dark-red	Totals
$F_1 \times B$, No. 13	{ green	41	13	18	8	80
	{ yellow	20	5	0	0	25
105						
Expected	{ 39.375	13.125	19.688	6.563	
		{ 19.688	6.563	0	0	

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This Table shows that the ratio scarlet : deep scarlet : dark-red : deep dark-red is 6 : 2 : 3 : 1 in green plants and also, that scarlet : deep scarlet is 3 : 1 in yellow plants. Accordingly the genetic constitution of the plant used must have been **GgDDbbMm**.

5. *Green plant with light dark-red flower.*

The results are indicated in Table IX.

TABLE IX.

		Light dark-red	Dark-red	White	Totals
No. 14	...	45	20	14	79
„ 55	...	28	9	11	48
„ 14—2	...	48	33	25	106
„ 19 (1918)		65	38	36	139
Totals	...	186	100	86	372
Expected	...	186·00	93·00	93·00	

From the above Table we see that the ratio light dark-red : dark-red : white is 2 : 1 : 1. Let us now consider what should be the genetic constitution of the plant used. From the explanation of the results in F_2 (Table II) we know that there should be six different genetic constitutions in plants with light dark-red flowers. But our hypothesis assumes that when **G** is in homozygous condition in the presence of **D**, the effect of **B** is not manifest, so that in this case, the result is quite the same, whether **B** is present as **BB**, **Bb** or **bb**. Consequently, the genetic constitution of the four families above mentioned must correspond to either one of **GGDdBBMM**, **GGDdBbMM** or **GGDdbbMM**; and in order to determine which of these three is the actual one, the hybridisation experiments with other families would be necessary.

6. *Yellow plant with light magenta flower.*

The results are indicated in Table X.

TABLE X.

	Light magenta	Magenta	Light scarlet	Scarlet	White	Totals
No. 39—1...	47	26	19	6	40	138
Expected ...	51·750	25·875	17·250	8·625	34·500	

From the above Table it is quite evident that the ratio light magenta : magenta : light scarlet : scarlet : white is 6 : 3 : 2 : 1 : 4, so that the genetic constitution of the plant used must have been **ggDdBbMM**.

7. *Yellow plant with magenta flower.*

The results are shewn in Table XI.

TABLE XI.

	Magenta	Deep magenta	Scarlet	Deep scarlet	Totals
No. 39—7 ...	64	22	22	10	118
Expected ...	66.375	22.125	22.125	7.375	

In the above Table we see that the ratio magenta:deep magenta:scarlet:deep scarlet is 9:3:3:1. Thus the genetic constitution of the plant used must have been **ggDDBbMm**.

8. *Yellow plant with light scarlet flower.*

The results are shewn in Table XII.

TABLE XII.

	Light scarlet	Scarlet	White	Totals
No. 22—4—6 ...	32	14	15	61
„ 22—4—10 ...	17	14	8	39
Totals ...	49	28	23	100
Expected ...	50	25	25	

Thus the ratio light scarlet:scarlet:white is 2:1:1, so that the genetic constitution of the plants used must have been **ggDdbbMM**.

9. *Yellow plants with dark-red flowers.*

As was reported in my previous paper¹, I found in F_4 a family (44—6) which, in spite of the fact that it segregates into green and yellow plants, yet breeds true to dark-red flowers; evidently there must exist some special reason for this fact, and the experimental results conducted on this family in F_5 are as follows:

TABLE XIII.

	Leaf colour in F_4	Leaf colour in F_5	Dark-red
No. 44—6—2	Yellow	Yellow	81
„ —4	„	„	25
„ —10	Green	Green	40
„ —7	„	{ Green	22
		{ Yellow	6

The above Table shews that all the families have dark-red flowers in spite of their yellow leaf-colour. What then, we may ask, is the cause which has led to such contradictory results? Now let us consider in

¹ *Journal of Genetics*, Vol. viii. No. 1, p. 73.

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detail the ancestors of these families. The seeds of these families were taken from the individuals which segregated in the following manner in F_3 :

		Scarlet	Deep scarlet	Dark-red	Deep dark-red	Totals
No. 44	green	13	9	9	8	39
	yellow	6	5	0	0	11
						50

The family 44—6 was the offspring derived by self-fertilisation from a plant having green leaf and dark-red flower. Consequently if the hereditary behaviour of these characters were normal we should have in the offspring leaves which are constantly green and flowers which are either constantly dark-red or will segregate into dark-red and deep dark-red. The results, however, have shewn that notwithstanding the fact that the flower-colour is constantly dark-red the leaf-colour segregates into 3 green and 1 yellow. So that it may be considered that there occurred some permanent variation among the factor or factors in the F_3 plant used for self-fertilisation. But we cannot decide how and where such change has occurred, and any hypothesis on this point would be useless unless founded on the facts actually obtained, so that this case will remain the subject of my future study.

IV. HYBRIDS BETWEEN A OR B WITH A RACE C WHICH HAS YELLOW LEAF AND DEEP DARK-RED FLOWER.

In all cases described till now there were found no yellow plants with dark-red flowers, except the case given above. Such a plant, however, is found among certain races of Japanese *Convolvulus*, and it seems to have been in cultivation more than 60 years ago, as it is described in a book entitled *Santo Ittyô* published in 1854, in which many coloured figures are found. My material is characterised by having the "hukurin" part on the margin of the flower. Although I have described the flower-colour of this race as deep dark-red, I found that certain differences are discernible between B and C , inasmuch as the colour of the latter is a little darker than that of the former. They are, however, so similar to each other that this slight difference would not be noticeable without direct comparison.

1. $A \times C$ and $C \times A$.

a. F_1 generation.

In both reciprocal crosses I obtained exactly the same results, the leaf being yellow and the flower light magenta. The "hukurin" appeared in quite the same manner as in the parent C .

b. F₂ generation.

All the individuals had yellow leaves. As in the case of $A \times B$ we obtained here also flowers of magenta, scarlet, and dark-red colour, and moreover there were found the three usual tones in each. All plants with coloured flowers had the "hukurin" on the corolla. It must be said that all the tones of flower-colour in $C \times A$ are somewhat different from those of F_2 plants in $A \times B$, and moreover, that the magenta and scarlet colour are slightly more blue-tinged in the former than in the latter.

The results of both reciprocal hybridisation are shewn collectively in Table XIV.

TABLE XIV.

	$A \times C$	$A \times C$	Totals	Expected
Light magenta ...	33	36	69	69.563
Magenta... ..	16	20	36	34.782
Deep magenta ...	14	23	37	34.782
Light scarlet ...	13	16	29	34.782
Scarlet	7	10	17	17.391
Deep scarlet ...	7	9	16	17.391
Light dark-red ...	15	19	34	34.782
Dark-red	11	11	22	17.391
Deep dark-red ...	8	9	17	17.391
White	44	50	94	92.750
Totals	168	203	371	

It will be readily seen from the above Table that the results are altogether similar to those of $A \times B$.

*2. B × C.**a. F₁ generation.*

F_1 plants had green leaves with deep dark-red flowers.

b. F₂ generation.

The flower of all F_2 plants was deep dark-red, and the leaf-colour segregated into green and yellow. As previously mentioned, there was a little difference between the flower-colours of B and C , and this difference appeared in F_2 , but as it was extremely difficult to distinguish them clearly I did not undertake to do this work. I will only mention here, however, that also in yellow plants the flower-colour similar to that of B parent has been observed. The results are indicated in Table XV.

In the above Table we see that the ratio green, "hukurin":green, fully-coloured:yellow, "hukurin":yellow, fully-coloured is 9:3:3:1, so

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that it may be seen that the leaf-colour and the "hukurin" are inherited in a simple Mendelian fashion.

TABLE XV.

		Number 1	Number 2	Totals	Expected
Green	{ white-margined ...	48	31	79	75.938
	{ fully-coloured ...	18	9	27	25.313
Yellow	{ white-margined ...	14	7	21	25.313
	{ fully-coloured ...	6	2	8	8.438
Totals ...		86	49	135	

From the results of $A \times C$, $C \times A$, and $B \times C$ it is clear that the genetic constitution of the C parent is **ggDDbbmm** with respect to the leaf- and flower-colour. Yet if we will speak more strictly there may exist some differences as regards the factor **D** between B and C , but I did not undertake to study these differences.

It is quite clear from the above results that C has a factor to produce the "hukurin" on the corolla; moreover that this factor is present in A but not in B has been fully confirmed.

V. SOME FACTS OBSERVED DURING THE EXPERIMENTS.

1. *Relation between the colour of flowers and that of other parts of plant.*

Many observations have already been made by several authors as regards the relation between the colours of flowers and those of other parts of plant. The phenomenon most commonly known is that where positive relations exist between them. Gregory¹ observed in *Primula sinensis* that anthocyanin may be entirely absent when the stem is green and that pale flower-colour is associated with faint colour in young leaves as well as green or faintly coloured stem; besides, he has discovered the following associations: deep flower-colour and deep stem-colour, true red flower-colour and true red stem, blue flower-colour and blue stem. Nohara² observed in his study of inheritance on *Oxalis corniculata* that the purple colour in the eye of the corolla and in the leaf are associated to each other, but the leaf-purple can appear without being associated with the eye purple. I³ have reported in the garden varieties of *Rhododendron obtusum*, *Rh. ledifolium* var. *purpureum*, and *Rh. indicum* var. *macranthum* which are cultivated in Japan, that the more intense the

¹ *Journal of Genetics*, 1911, Vol. i. pp. 73—132.

² *Journal of College of Agriculture*, Tôkyô, 1915, Vol. vi. pp. 165—181.

³ *Journal of the Scientific Agricultural Society*, Tôkyô, 1914, No. 145, pp. 1—6.

reddish-brown colour of winter leaves are, the deeper the flower-colour is; besides I have reported that white flower-colour is associated with green leaf, and striated flower with striated leaf.

The above statements shew that the colours of flower and leaf or stem are due to one and the same factor. There are some cases, however, where the colour of flower and that of other plant-organs seem not to be determined by one factor. Shull¹ found in the hybrids between *Oenothera rubricalyx* and *rubrinervis* and those between *rubricalyx* and *Lamarckiana* that pigmented buds of *rubricalyx* is invariably associated with a low degree of pigmentation in stems and rosettes. Besides these, many other examples were reported in *Primula sinensis*, *Helianthus* and *Lathyrus*, etc.

In the Japanese *Convolvulus* white flowers may be associated with green or yellow stem, and coloured flowers with pigmented stem. In my experiments the stem-colours in plants with deep-coloured flowers were found to be deeper than in those of light-coloured individuals, and moreover the stems of plants with dark-red flowers were dark-reddish-brown and those of scarlet flowers were reddish-purple. But I could not discern the differences of stem colours between plants with magenta and those with scarlet flowers. Thus the relation between the colours of stem and flower is similar to what we see in *Primula sinensis*.

2. On streaked flowers.

Though there are many investigations on the inheritance of streaked flowers in *Antirrhinum*, *Mirabilis*, etc., I will mention here simply the facts observed in Japanese *Convolvulus*. In and after the F_2 generation I have often observed that just one half of a petal to the throat produced a colour entirely different from that in other parts. Such phenomenon did not occur in all flowers of a plant but only in one or two out of fifty or more. Thus I have seen a light magenta part in a light scarlet flower, a magenta part in a scarlet flower, and a deep magenta part in a deep dark-red flower. These are the instances where the dominant colour was produced in a recessive coloured flower, though I have once seen a deep scarlet part in a deep magenta flower, i.e. recessive colour in dominant coloured flower.

Emerson² studied the occurrence of anomalous seeds of maize as regards their pigmentation. In one case, the seed was half colourless

¹ *Journal of Genetics*, 1914, Vol. iv. pp. 83—102.

² *Zeitschrift für induktive Abstammungs und Vererbungslehre*, 1915, Bd. xiv. pp. 241—259.

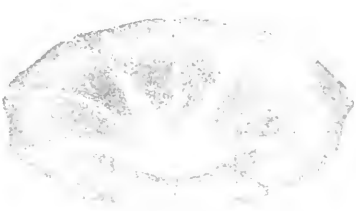
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and half purple; in the other, half purple and half red. His opinion on the occurrence of this phenomenon is that it is due to a somatic mutation, that is a change in genetic constitution rather than a segregation of genetic factors, and this somatic mutation may be a gain of at least one new factor, the loss of a factor, or the permanent modification of a factor. Moreover he brings against the segregation hypothesis the following considerations. "If a dominant character appears as a bud sport, in material known to be homozygous with respect to a recessive character that is allelomorphic to the dominant character in question, it seems clear that a somatic mutation is the responsible agent....It would be interesting to know whether recessive bud sports actually occur much more frequently in heterozygous than in homozygous material. If this is found not to be the case, it will have an important bearing upon the problem of whether bud sports are mutations or segregations, for the latter would occur only in heterozygous material."

Above we have described three cases of Japanese *Convolvulus* where the dominant character has arisen in material known to have the recessive characters. Accordingly it is impossible to consider this phenomenon merely due to the segregation of factors, but it will be necessary to think that there occurred some change in the somatic cells which have had recessive characters. I did not cultivate the offspring of the plant which produced a deep scarlet coloured part in a deep magenta coloured flower, so that I cannot decide whether the original colour was in a homozygous or a heterozygous condition. If in the latter condition we may consider the phenomenon due either to the segregation of factors or to somatic mutation, but if in homozygous condition the latter would seem to be the real cause of the phenomenon.

3. *The relation between leaf-colour and the growth habit of plant-body.*

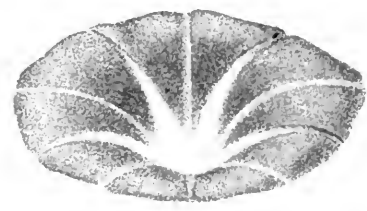
The parent *B*, which has green leaves, grows vigorously. It has a big and long stem with long internodes, and side branches appear at the fifth or sixth leaf axil from the base. *A* on the other hand has a slender stem with side branches appearing at the second or third leaf-axil and flowers opening earlier than *B*. The F_1 plant has characters similar to those of *B*, at least as regards the above stated points. In the F_2 generation also these characters were found to be associated with the leaf-colour, though I did not undertake to measure. It is quite clear that the weak growth of yellow-plant is due to small amount of green pigment in them.



1



2



3



4



5



6



7



8



9

SUMMARY.

1. The light magenta colour in F_1 is produced when both **G** and **D** are in heterozygous condition; and the bluing-factor **B** and the modifying factor **M** are brought in from the parent **A**.

2. Reciprocal hybrids are similar to each other in all respects.

3. **D** produces dark-red colours when **G** is present in a homozygous condition, but it produces red-colours (magenta and scarlet) when **G** is present in a heterozygous condition or altogether absent. Such an inter-relation between **G** and **D** was found only in the hybrids between **A** and **B**, and it does not exist in other hybrids, though **C**, for instance, has colours closely related to those of **B**.

4. The fact that **D** has such a character may be seen closely from the results in which all three families of the offspring of $(10-1) \times (16-9)$ which is green, white and yellow, deep scarlet, respectively, produced dark-red colours.

5. The effects of **B** are not manifested in the individuals which are in a homozygous condition with respect to **G**.

6. The magenta colour appears in plants which have the constitution **DB**, either **Gg** or **gg** being present at the same time. On the contrary, the scarlet colour appears only in plants which are in the condition **Db**.

7. The white colour appears in the individuals when **D** is altogether absent, and then **G**, **B**, and **M** may be in any condition. So that there are various genetic constitutions among white-flowered plants.

8. The interrelations between **D** and **M** are as follows:

DdM	light colour
DDM	medium colour
DDmm }deep colour
Ddmm }	

9. The magenta colour is dominant over both scarlet and dark-red, and scarlet is dominant over dark-red.

10. There may exist homozygous plants, at least with respect to flower-colour, with medium and deep tones of magenta, scarlet, and dark-red; but we could find no individuals with light tones of each colour.

EXPLANATION OF PLATE I.

Figs. 1, 2, 3. Light, medium, and deep magenta.

Figs. 4, 5, 6. „ „ „ scarlet.

Figs. 7, 8, 9. „ „ „ dark-red.

A GRAFT-INFECTIOUS DISEASE OF DATURA RESEMBLING A VEGETATIVE MUTATION.

BY A. F. BLAKESLEE,

Station for Experimental Evolution, Cold Spring Harbor, N.Y.

(Received May 15, 1920.)

(With Plates II—VI.)

I. INTRODUCTION.

AT the New York meeting of the Botanical Society of America in 1916 the writer presented a paper entitled "A Recurrent Mutation in *Datura* Suggesting Vegetative Segregation." As reported at the next meeting of the Society, more recent experiments have shown that the peculiarity is in the nature of a disease since it can be transmitted by grafting upon normal stock. The variation involved, among changes in other morphological characters, a suppression of spines on the capsules. As observed by earlier geneticists, it had been assumed to have resulted from imperfect dominance of spininess when the normal type was crossed with a smooth-capsuled variety. In as much as the disease is transmitted through both seed and pollen and causes profound morphological changes in the individuals affected, it at first appeared to be genetic in nature. It seems appropriate therefore to publish the present paper in a journal of Genetics rather than in one devoted to phytopathology with the thought that results obtained in *Datura* may be of possible value to geneticists in explaining peculiarities in their breeding experiments with other species.

The Jimson Weed, *Datura Stramonium*¹, is historically of interest to students of heredity, since before the appearance of Mendel's work

¹ A number of species have been established based on forms which differ genetically from *D. Stramonium* by single factors. Thus *D. Tatula* is the purple spiny form, *D. laevis* of Naudin and *D. Bertolonii* of Godron is the white, smooth-capsuled form. The contrasting pairs of genetic characters so far discovered are spiny and smooth capsules, purple and white flowers associated with purple and green stems, and many and few nodes between the cotyledons and the first fork. We have preferred to include under the name *D. Stramonium* all the forms which differ by single Mendelizing factors as well as various named biotypes which differ from *D. Stramonium* at best in minor characters chiefly of leaf and habit.

on peas, Naudin (7) and Godron (6) had used this species in studies of inheritance and with it had discovered the reappearance of the contrasting parental types in the F_2 generation. De Vries (8) and later Bateson and Saunders (2) used the same species soon after the re-discovery of Mendel's Law in studies on the inheritance of spininess and colour. The present writer with Avery (4 and 5) has also accumulated additional data on the inheritance of these and other characters.

Plants showing the disease have been called Quercina (abbreviated to Q.) on account of peculiarities in leaf structure. The first Quercina plant was found in cultures at the Conn. Agric. College in the fall of 1915. It was considered a spineless mutant of the purple-stemmed form. Two open-pollinated capsules had set, and two flowers later opened, which, since their stamens were devoid of pollen, were artificially pollinated by other plants. The seed thus obtained was the origin of a series of breeding experiments with the Quercina mutant as it was then called.

II. DESCRIPTION OF QUERCINA PLANTS.

In describing the distinguishing characteristics of Quercina plants it will be convenient to start with seedlings from the open pollinated capsules obtained in 1915. As will be shown under breeding experiments, Quercina plants do not breed true, but throw a small proportion of normals along with Quercina seedlings. The latter usually can be recognized at an early stage, sometimes as soon as the cotyledons have expanded. Pl. II, fig. 1 shows above three Q. plants in 3-inch pots in contrast with three below from the same pedigree which were considered normal at the time the photograph was taken. The early leaves of Q.'s tend to be narrower than normals, more or less twisted, and with indentations at the margin. Pl. II, fig. 2 shows the same plants at a later date but similarly arranged. The increasing indentation of the leaves in comparison with the normals is evident. The plant at the lower left-hand corner which previously was classed as normal has now shown its Q. nature by the character of its later leaves. At times, Q. seedlings appear normal till a relatively late stage, but in general a seedling which has the character shows it early.

A series of Q. leaves are shown on Pl. IV, fig. 5 below in contrast with a series of normal leaves above from the same line. The marked indentation of the leaves shown in the photograph is not an extreme condition. The leaves on some Q.'s may be eroded so far as to leave

little more than the mid-ribs. If the Globe mutant, which has broad leaves, becomes Q., the leaves become narrower than typical Globes, but are still broader than normal narrow-leaved types. An increased indentation, however, is characteristic of all Q. leaves, whatever may be the genetic type to which the plant belongs.

The stature of Q. plants is somewhat less than that of normals. The branches are more slender and the root system is less well developed.

Typical Q. flowers are recognizable at an early stage. A series with buds is shown on Pl. III, fig. 3 in comparison with normal flowers below. The corolla of Q. flowers is split between the lobes as far down as the insertion of the filaments as shown in the opened flower on the extreme right from which the calyx has been removed. The corolla segments are incurved and twisted around the base of the flower. Frequently in the expansion of the bud they are unable to free themselves from the calyx. The third and fourth Q. buds from the left are typical of such "blind" flowers which may fall from the plant without opening. The infolding of the lobes is characteristic of early stages, and hence, when a normal bud would have its corolla nearly reaching the tip of the bud, the incurved lobes leave an empty space inside the apex of the calyx at the stage shown by the second bud from the left. The flowers of purple Quercinas are darker coloured than normals and the stem colour in such forms is also increased in intensity.

The stamens in the bud (Fig. 4) are found to be shrivelled, and in typical Q.'s produce nothing more than a few small grains which when tested have been found to be functionless.

The stigma in normal plants is made up of two thick lobes, facing outward (Fig. 4). In Q. flowers the stigmatic surface is chiefly on the inside of the lobes and runs part way down two sides of the style.

The most conspicuous peculiarity of Q. plants, however, is the suppression of spines on the capsule. This may be complete, giving capsules as smooth as those of the *inermis* variety. The form of the capsule, however, is that characteristic of the variety or mutant affected, the globe mutant plants, if also Q., having flattened globose fruits. Seeds from Q. capsules are distinctly smaller than those from normals and their percentage of germination is less. The cotyledons are frequently unable to extract themselves from the seed coats without assistance and plants may die for this reason. Older seedlings also appear to be less vigorous than normals.

III. . ORIGIN OF QUERCINAS IN THE FIELD.

The description which we have given of Q. plants is based on individuals which had come from Q. seed. The condition, however, breaks out in the field, generally late in the season on plants which have been produced by normal parents. The infection may be first noticed weakly expressed in a single branch, and gradually spreads as new growth occurs. Fig. 6 is a photograph of such a branch which has a normal spiny capsule at the lowest fork shown. The later capsules show a gradual suppression of spines to the one which is entirely smooth. Occasionally an infected capsule is found with one or more of the four valves smooth and the rest spiny as shown in Fig. 7 (insert. in Fig. 6). The two flowers of the infected branch, above and at the right, have the characteristic separation of the corolla into segments.

The presence of the disease may be first observed in the change in form of leaves and flowers. Purple flowers become darker in colour and often slightly mottled with lighter patches, before the infection has brought about a splitting of the corolla. As the season advances more plants show Q. branches. When normal plants have flowered and formed capsules, Q. plants are still flowering; for the Jimson Weed is normally self-pollinated in the bud, and Q. plants, from their lack of pollen, are dependent for setting capsules upon occasional off-pollination which is especially rare in such plants on account of the failure of many flowers to open.

Table I shows the number of Q. plants found in normal and Q. pedigrees in the field for the year 1916. In 1917 in the same field there were 1.67% spontaneous occurrences of Q.'s out of 5230 individuals planted in the ordinary manner. No Q.'s from seed were planted in the plot this year.

With only a single possible exception have Q.'s ever been observed to occur spontaneously in the greenhouse, where Q. plants as well as normals were under cultivation. Under greenhouse conditions plants are not grown as large as in the field. This fact would give a lessened opportunity for infection, but in the many thousand plants infection would have been expected in a few if the means of transmission were present. It is perhaps similarly because of the lack of means of transmission that Q. infections have been rare in our plots near the greenhouses, while a mile away in our hill plots they have been common. Thus, while in 1917 there were 1.7% in the 5230 plants in the regular hill plots, there were no infections in over 2000 plants in the plots

near the station, including pedigrees planted close and far apart. There were at this time also 88 Q. seedlings planted in the station plot.

In that year representatives of certain of the pedigrees were grown in a "spread" plot with the individuals spaced five feet apart. Plants in these spread plots had an extremely high percentage of incidence (26.4 % out of 167 individuals), while plants from the same pedigrees elsewhere in the field, but spaced the customary one foot apart, showed only the usual proportion of Q. plants (1.6 % out of 643 individuals). The larger number of Q.'s in the spread plots may have been due to the relatively enormous size of these plants which were not reduced in growth by their neighbours. Each plant therefore gave a greater area exposed to infection, and infection once taking place was carried to all the numerous branches of the plant. Infection on the branch of a plant in the more crowded plots, on the other hand, was apparently unable to infect more than the few branches organically connected with it since plants adjacent to Q.'s and with their branches touching seem no more likely to acquire the infection than if adjacent only to normals. What the carrier of the virus may be is at present unknown but evidence beside that just given leads to the belief that the Q. disease is not communicated by mere contact.

Apart from its appearance in our cultures, we have found Q. plants upon two occasions. Once in Staten Island where several such plants were discovered, and once at Woodbury, Long Island, where a single Q. plant was found among a group of 182 normals. One out of five seedlings from the latter plant was a Q., but none of the four seedlings from the Staten Island material turned out Q. The writer has inspected relatively few *Daturas* growing wild. It is probable that a more careful search would show the disease not uncommon in wild plants.

IV. BREEDING EXPERIMENTS.

(a) *Inheritance of Q. through Female Gametes.*

While it was still thought that Q. was a genetic mutant, a considerable amount of breeding work was carried on combining it with all the available types of Jimson Weeds. No varietal immunity has been discovered within the species. From the four capsules produced by the first Q. plant discovered in 1915, 120 seedlings were produced, of which 53 were normal and 67 Q.'s. Breeding work with typical plants of the latter class was carried on in the greenhouse in 1915-16.

Since the typical Q.'s are devoid of pollen it has been necessary to cross them with normals. Table I (p. 32) shows the results of such crosses from field records of 1916. Q.'s are produced in 79 % of the offspring of Q. female parents. The remaining normal plants from Q. parents do not carry the infection. The incidence of spontaneous infection in the field was even somewhat less for them (0.95 %) than for normals free from Q. ancestry (1.26 %).

Q. plants from Q. parents usually show their Q. nature at an early seedling stage. In 1916 the seedlings from Q. parents were labelled "Normal," "Questionable," or "Quercina" at the time of setting into the field from 3-inch pots. When the adult plants were inspected in the fall, their condition was compared with the earlier records on the pegs that remained. The results are tabulated in Table II (p. 32).

Plants classified as Q.'s in seedling stage are Q.'s when adult. The two exceptions noted out of 671 plants, if not the result of experimental error, may be due to faulty classification in the earlier record. It will be noted that in seedlings the Q. infection is determined by leaf abnormalities alone. Apart from these two possible exceptions we have not observed that the plants once infected ever recover. The infection often manifests itself, however, only after the plants have been transplanted to the field, as is shown by the 17 % of apparently normal seedlings which later became Q.'s. There is usually little difficulty in distinguishing Q. plants out of infected seeds from field infected individuals, in which the character is evident later in the season and does not involve the older leaves. About as many "Questionable" seedlings turned out normals as there were normal seedlings which turned out Q. If all the questionables were included with the Q. seedlings they would have given in consequence a close approximation to the total Q.'s found in the adult stage.

Some of the plants put into the field died before final records were taken, and some of the labels were lost. The table includes only individuals with complete records. Of 77 plants not included in the table which died in the field, 24 were described on the pot labels as Q.'s, 51 as Questionables, and two only as normals. In other words 3.4 % of the seedlings classified as Q.'s died in the field, 12.8 % of those classified as Questionables, and only 0.7 % of those classified as normals. The questionables were probably thus classified on account of not having developed far enough to allow a sure identification of their character. They were thus weaker plants when set out, hence their greater mortality. If we class all the Questionables with the

Q.'s we have a mortality of 6.8 % in Q.'s against 0.7 % mortality in normals. Whatever the figures used, the infected plants are seen to be less likely to survive than normals. As will be noted later, the per cent. of germination of Q.'s is lower than that of normals, hence the final records fail to indicate the total amount of seed infection. The breeding evidence shows, however, that the Q. infection is carried by the female gametes and affects at least 79 % of the seed produced by Q. parents.

(b) Investigation of Two Field-infected Plants.

In the 1916 field cultures two plants (*A* and *B*), which had become spontaneously infected and which showed the infection in different degrees in individual branches, were chosen for detailed study. The problem was to ascertain if any relation existed between the proportion of Q. offspring and the strength of the Q. character measured by the relative number of spines on the capsules from which the seedlings were derived. A smooth capsule was graded 0, and one fully armed was graded 4; 1, 2 and 3 were intermediate grades from very slightly spined to a condition with spines somewhat reduced below normal. Final records were taken of the potted plants between four and five months after planting. A considerable number of individuals were not graded on account of late germination, or on account of doubtful determination at the time it was necessary to clean out the greenhouse for other cultures. If such doubtful plants had been retained to a recordable size they would probably have increased the percentages of Q.'s. All plants that germinated however, have been included in figuring the percentages of germination. The capsules of plant *B* were all open pollinated, those of plant *A* were part open pollinated and part pollinated by hand. Tables III and IV (p. 33) give details for the two plants, and Table V (p. 34) gives summaries. Although some individual inconsistencies occur, it will be observed that the capsules which show evidence of infection give a higher percentage of Q. seedlings and a lower percentage of germination than capsules which appear normal.

A number of the capsules of plant *A* showed unequal distribution of spines on the four valves of the type shown on Pl. IV, fig. 7. Seeds from individual valves were sown separately with the result shown in Table VI (p. 34). Valves *A* and *B* form one carpel, and *C* and *D* form the other, of the two-celled ovary. In some cases only a part of the seeds was sown separately from the individual valves, and therefore

the numbers in Tables III and VI are not in all cases identical. A correspondence between the percentage of Q. seedlings and the amount of spininess of valves from which they were derived is scarcely evident.

We conclude that the percentage of infection of the seed is only very roughly proportionate to the external evidence of the disease on the part of the plant from which they were derived and that the correspondence largely if not entirely disappears in reference to the divisions of individual capsules. In other words, if a capsule from a plant which is becoming Q. is fully armed and thereby shows no external evidence of infection, its seedlings are relatively low in Q.'s. On the other hand, if the capsule shows evidence of reduction of spines recognized by the grades employed, the seedlings are relatively high in Q.'s. So long as the capsule appears to be infected at all, the grade of spining has no close relation to the percentage of Q.'s in its offspring.

(c) *Inheritance of Q. through Male Gametes.*

It has been shown that the Q. infection is strongly transmitted through the female gametes. The question arises as to whether it can be carried by the pollen. A difficulty lies in the fact that typical Q. plants are devoid of pollen. Occasionally, however, as a plant becomes infected in the field, some of the flowers may not be so strongly affected as the rest and in consequence may produce a varying amount of pollen. This was the case with five flowers of plant A already discussed. Table VII (p. 34) shows the proportion of Q. and normal offspring when the infection is carried by the male gametes. The pollen from flowers A 11, A 12 and A 15 was only slightly potent in transmitting the disease, as might be expected from the grade of their capsules, while the flowers A 7 and A x were more active. Unfortunately the record on flower A x is not complete. It is evident that these flowers which throw few Q.'s when selfed do not actively transmit the disease through the pollen, while A 7 transmits the disease actively both when selfed and when the infection is carried through the pollen. The high proportion of Q.'s from the self of A 15, the pollen of which was inactive, may have been due to an infection of the pistil which had not yet involved the stamens. Why pedigree 16655 should run so high in Q.'s is not clear unless a single anther of the flower was strongly infected and happened to be used in making the cross. It cannot be determined from our present records whether pollen was taken from individual anthers or mixed in making these crosses.

The experiments show that the male gametes can carry the Q.

infection. Since Q. pollen infects the seed, it doubtless would infect the tissues of the plant when carried to flowers of normal plants. Insect pollination might be one means of the spread of the disease from lightly infected individuals with functional pollen.

V. INOCULATION AND GRAFTING EXPERIMENTS.

The spontaneous appearance of Q. branches on field-grown plants and the spreading of the character to new branches of affected individuals suggested that the peculiarity was in the nature of a disease. In testing this supposition a series of inoculation and grafting experiments were undertaken.

(a) *Inoculation Experiments.*

One of the commonest diseases of tobacco, another member of the *Solanaceae*, is "mosaic" or "calico" as it is called from the patches of lighter colour on the leaves. The causal organism is not known, but the infection is readily communicated from one plant to another by mere contact of healthy plants with infected leaves. Mosaic diseases of unknown nature have been discovered in other groups. It was thought that the Q. complex might be due to such a mosaic type of disease. Accordingly attempts were made to transmit the infection to healthy plants by rubbing their leaves with those of Q. plants, and by needle inoculations with the expressed juice of Q. leaves, but without success. In one experiment two cions from normal plants were left in the expressed juice from Q. leaves for 24 hours, and two other cions for 48 hours, before grafting them on to normal stock. Neither of these four cions took the disease nor caused the normal stock to turn Q. Transmission of mosaic diseases by contact in other species is often difficult of accomplishment and it is possible that more extensive trials would have given occasional success with the Q. disease of the Jimson Weed. However, mere contact of leaves cannot be a usual means of infection in nature, since in the field normal plants, adjacent to Q.'s and with their leaves touching, seem no more likely to be infected than those adjacent only to normals. The disease is easily transmitted, however, by grafting.

(b) *Grafting Experiments.*

Grafting of Q. branches on normal stock or the reverse union invariably has given infection. This has often resulted even when the Q. cion has died and dropped off before a perfect union has been established. Pl. V, fig. 8 is a photograph of a green-stemmed normal

plant. Its two main branches were cut off a short distance above the fork and on the left branch was grafted a purple Q. cion, recognized by its eroded leaves, and on the right branch was grafted a purple normal cion. The infection passed down the one branch and up the other into the normal cion, causing the production of a capsule with a reduced number of spines and a later capsule entirely smooth. The buds in the stock below the fork also grew out with Q. characters, the one on the left shows a single capsule with reduced spines and one entirely smooth while the one on the right shows a single capsule likewise entirely smooth. The infection is usually manifest as soon as new leaves are formed and gradually spreads leaving the older parts, produced before the infection, free from abnormality and causing the new growth to be more and more distinctly Q. in appearance.

A number of other Solanaceous species, including several different genera, were tested by grafting with Quercina Jimson Weeds. None was found to be so susceptible to the disease as the Jimson Weed, however.

Datura meteloides could be infected by grafting, but the disease was slow in showing. The disease could be brought back to the Jimson Weed by grafting on it a cion of infected *D. meteloides*. In Pl. V, fig. 9 a cion of this species is shown grafted on the normal Jimson Weed at the left (marked *Nor.*) and a cion from the same plant was grafted on the Q. plant on the right (marked *Q.*). The infection of the *D. meteloides* shows as a mottling of the leaves with lighter patches and a puckering of the leaf surface. This was the condition three or four months after the graft. A few months later the leaves of the cion were free from abnormal colour and puckering of their surfaces, but had their margins deeply eroded. On such plants the flowers are devoid of pollen. Three of such infected flowers were pollinated from a normal plant of *D. meteloides* and selfed seed from the pollen parent were taken as a control. In comparison with the 10 individuals in the control, the 291 seedlings from the Q. capsules of *D. meteloides* were obviously stunted and their leaves of a paler colour. By the time of flowering, however, all of the 291 plants had recovered and showed no trace of infection except one, which had lacerated leaves, flowers without pollen, and somewhat eroded corollas. This plant, No. 18182 (1) is shown at the left in Pl. VI, fig. 10 beside a normal plant from the same pedigree. The Q. disease is therefore not so readily transmitted through the seed in *Datura meteloides* as in *D. Stramonium*, although the former species acquires the disease slowly through graft infection.

Most of the species tested seem immune to the infection and unable to transmit the virus. The *Petunia* is a typical example. In addition to controls, eight attempts were made to infect this species by grafting with *Q. Jimson Weeds*, but without success. In one case, shown in Pl. VI, fig. 11, a *Petunia* cion was grafted on a *Q. Jimson* stock (*Q.*). A month later a cion from a normal *Jimson* (*N.*) was grafted on to the *Petunia*, leaving a distance of 16 cm. between the two grafts. Five and a half months after the last graft was made the *Jimson* cion at the top of the plant was still normal in appearance, and had produced two spiny capsules while the original stock was still *Quercina*. Twenty-six seeds from the second of these capsules were planted and produced 20 seedlings, all normal. It may be concluded that the *Petunia* neither acquires the disease, nor is able to transmit the virus through as much as 16 cm. of its stem.

An experiment similar to that just described for the *Petunia* was tried with the tomato. The virus failed to pass through 3.5 cm. of the tomato stem and infect a normal *Jimson* graft above it. It is possible that with a shorter distance the experiment would have succeeded, since, in one out of three trials, a cion taken from a graft on a *Q.* plant gave the disease to a normal *Jimson* when grafted on it. In this case, however, the cion was cut off from very near the junction between the tomato and the *Q.* stock, and it is barely possible that some of the tissue of the latter was the cause of the infection.

Both the two cions of Jerusalem cherry grafted on *Q.* stock produced normal flowers with pollen and fruit, but their leaves, although normal in shape and otherwise like the controls, were more or less blotched with yellowish patches. Of two grafts from these infected cions on to normal *Jimsons*, one transmitted the disease and the other did not.

The egg-plant gave some evidence of being susceptible to infection. Two cions were grafted on to *Q. Jimsons*. One grew but slightly and hence had little opportunity to show the disease. The other cion produced a vigorous growth, with many flowers with pollen and finally fruited. The leaves were normal in shape, but were puckered in a manner shown by the earlier stage of infection in *Datura meteloides*.

The only instance not already mentioned where a species showed any evidence of being susceptible to *Q.* infection through grafting was with *D. Ceratocaula*. Of two cions grafted on to *Q. Jimson* stock, one produced a flower without pollen and also two slightly abnormal buds which fell off before opening. These latter buds had their corollas more or less slit. Later flowers from this plant, however, were normal.

Except for the abnormalities of these three flowers in a single plant the cions were normal in appearance.

In Table VIII are listed the species tested by grafting with Q. Jimson stock. Controls on normal Jimsons were tried in all cases.

At least one other mosaic-like disease has been found infecting Jimson Weeds. This has been called "Z." It was first noticed in two adjacent plants in the field cultures of 1917. Pl. VI, fig. 12 is a photograph of an infected individual. Infected plants are obviously diseased. The leaves are light in colour, mottled, more or less eroded, and strongly puckered resembling somewhat the badly diseased leaves of beans attacked by mosaic. The leaves may be reduced to merely the midribs. The capsules are deformed, with spines reduced or entirely absent. The buds are generally elongated, the flowers "confused" with corollas often split or otherwise malformed and with numerous accessory carpels frequently developed. Infection develops rapidly in the plant and soon renders it valueless for records or for the production of seeds. The disease was first serious in the field cultures of 1919. From its spread from centres of infection it was obviously transmitted by means of contact. Attempts to communicate the disease to normal plants by rubbing them with infected leaves were successful with some exceptions. No extensive experiments have been made with this disease to discover what other Solanaceous species are susceptible. It has not yet been found possible, however, to transmit it to the tobacco (*Nicotiana Tabacum*) either by rubbing the leaves together or by grafting.

From smooth capsules of a Z plant 89 seeds were sown and gave 77 seedlings which remained normal. The experiments indicate that the Z disease is infectious by contact of leaves but is not carried by seed.

VI. EARLY RECORDS OF QUERCINAS.

It has not seemed profitable to search all the early records for descriptions that would indicate plants with Q. infection. Naudin (7) and Godron (6), as well as Bateson and Saunders (2), undoubtedly had them under observation. It may be stated that the writer has grown many thousand plants of the Jimson Weed, including large numbers of individuals that were heterozygous for *inermis* capsules, but has never observed any except Q.'s which showed a mosaic arrangement of the spines on the fruits, with some valves smooth and others more or less spiny.

Naudin (l.c., p. 49) reports in an F_1 between an *inermis* variety (*D. laevis*) of *D. Stramonium* and the armed type, that while most of the plants had spiny fruits, others had fruits with reduced spines. Many of the capsules on three out of the 40 plants in this generation were very spiny on part of the surface while totally smooth on the rest. Naudin believed that they united thus by distinct and separate compartments the distinctive traits of the parental types (*D. laevis* and *D. Stramonium*). He calls this "*hybridité disjointe*" and cites in this connection the condition in the graft chimaera *Cytisus Adami*. He attempted to secure offspring from the smooth part of such a mosaic capsule, but due to the poor maturity of the seed only four seedlings were obtained. Of these, one was *inermis*, and may have been an extracted recessive or a strong Q. In a series of F_2 plants from the same original cross, Naudin found six individuals out of 38 which again showed more or less well marked his "*hybridité disjointe*" and which were also presumably Q's.

Godron (l.c., p. 14) reports finding capsules partly spiny and partly smooth. He objects to Naudin's interpretation that the separation of the fruit into smooth and spiny portions is due to their origin from smooth and spiny parents, since he says that he has found this condition when *both* parents had spines.

Bateson and Saunders (l.c., p. 23) after discussing the intermediate colour of the flowers of the F_1 between white and purple flowered forms say:

"The occurrence of intermediate forms was also occasionally noticeable in the fruits. Among the large number of capsules examined, there were some of the mosaic type, in which part of the capsule was prickly and the remainder smooth, while others, suggesting a blend, were more or less prickly all over, but the prickles were much reduced in size, and often formed mere tubercles. These mosaics occurred as rarities both on prickly individuals and on smooth ones still more rarely."

Further evidence pointing to the Q. nature of these abnormal capsules is given in their following statement:

"Such intermediate fruits were most often found towards the end of the flowering season."

In a footnote (l.c., p. 24) they call attention to a plant with a single undersized smooth fruit in the F_1 from the cross, purple *inermis* \times white armed, where only armed plants heterozygous for *inermis* should be expected. If their suggestion of possible experimental error for the appearance of this plant be not the correct explanation it may have

been a strong Q. which, both from competition with more vigorous normal individuals and from the difficulty of securing pollination, might readily be reduced to the production of but a single capsule. A single capsule on a normal plant in the field, however, would be rare under usual cultural conditions.

To one familiar with the manifestations of the Q. disease, it seems likely that the examples just given above from the literature are instances of infected plants rather than cases of blending or of so-called "mosaic" inheritance. The term "mosaic," however, may be applied to the disease, if not to the type of inheritance, since it resembles in many ways the mosaic of the tobacco, beans, and other forms for which a causative organism has not been discovered.

VII. DISCUSSION.

Mosaic diseases are not uncommon but their nature is obscure. A number have been described for the Solanaceae (cf. Allard (1)), and the mosaic or calico of tobacco is familiar to all who have grown the plant. The disease of the Jimson described in the present article differs from the others of the family in that it is carried by both seed and pollen and appears not to be transmitted artificially by mere contact or inoculation.

That grafting communicates the infection to normal plants relates the disease to infectious chlorosis of *Abutilon Thompsoni* and other forms investigated by Baur (3). It differs from such instances in that no vegetative function of the plant is obviously impaired. The strong Q.'s, which come from infected seed, although smaller than the normals, are as vigorous as many of the mutants. It also differs from infectious chlorosis of the mallows in that it is carried by seed.

The profound morphological changes brought about in the leaves and especially in the flowers and fruit are such that Q. individuals would be considered worthy of specific if not of generic separation if 100 % of the seedlings instead of only 79 % came true to the Q. complex. As the facts stand, however, there is much in the behaviour of Q. plants which suggests genetic phenomena.

VIII. SUMMARY.

1. A form called Quercina was discovered in the Jimson Weed (*Datura Stramonium*) occurring spontaneously like a mutation.

2. Quercina plants are distinguished from normals by greater dentation of the leaves, slitting of the corolla, absence of pollen, partial or entire suppression of spines on the capsules, and certain other characters associated with less vigorous growth.

3. In a single year's test about $1\frac{1}{4}\%$ of the normal plants in the field took on the Quercina character by the last of the season. The Quercina character generally shows itself weakly in a single branch and gradually spreads to all the new growth.

4. The Quercina complex is transmitted by seed to about 79% of its offspring when pollinated from normal plants. The remaining 21% normal offspring do not produce Quercina seedlings in the next generation.

5. There is a rough correspondence between the strength of Quercina character in the parent and the number of Quercina plants in its offspring.

6. In plants which were becoming Quercina, pollen was obtained which transmitted the character.

7. Quercina cions grafted on to normal plants of the Jimson Weed cause the new growth of the stock to take on the appearance of Quercinas.

8. The cause of the Quercina characters is a disease transmitted by grafting.

9. Certain other species of the Solanaceae were found to be susceptible to the disease by grafting though to a less degree.

10. It has not been possible to infect plants artificially by rubbing with diseased leaves nor by inoculation of expressed juice from Quercina plants.

11. Another disease of the Jimson Weed is briefly described which is highly infectious by contact.

12. Instances in the literature are cited where the same disease apparently has been recorded but mistakenly attributed to a vegetative segregation or "mosaic" inheritance brought about by smooth and spiny varieties in the ancestry.

TABLE I.

Quercina Jimson Weeds (Datura Stramonium). 1916 Records.

Origin of Cultures				Number of Seed Parents	Total Offspring	Normal	Quercinas	Percentage Quercina
(1) Washington, D.C. Inbred 5 generations :								
(a) Purple Armed (2 lines)				13	596	584	12	2.01
(b) White Armed (1 line)				4	260	258	2	0.77
(2) Erfurt, Germany. Inbred 4 generations :								
White Inermis (2 lines) ...				6	390	388	2	0.51
(3) Various Crosses (6 lines) within (1) and (2)				83	2845	2813	30	1.05
(4) Staten Island (4 lines) ...				28	770	748	22	2.86
(5) Bronx, N.Y. (4 lines) ...				4	694	689	5	0.72
(6) Cold Spring Harbor, N.Y. (1 line)				1	246	246	0	0.00
(7) All lines with Normal ancestry (15 lines)				139	5801	5726	73	1.26
(8) Normal Plants from Quercina Parents (1 line)				51	1781	1764	17	0.95
(9) Normal Plants (16 lines) Grand Total				190	7582	7490	90	1.19
(10) Quercina (1 line) crossed with Normals (5 lines)				34	1348	283	1065	79.01

TABLE II.

Comparison of Seedlings and Adults from Quercina Parents. 1916 Records.

Seedlings		Normal		Questionable		Quercina	
		Nos. ...	Percentage	Nos. ...	Percentage	Nos. ...	Percentage
		273	21.1	349	27.0	671	51.9
		N.	Q.	N.	Q.	N.	Q.
Adults ...		83.1	16.9	12.3	87.7	0.3	99.7
		Nos. ...	Percentage	Nos. ...	Percentage	Nos. ...	Percentage
		227	46	43	306	2	669

Totals ... In Adult stage, 79.0% = Quercina ; 21.0% = Normal.

TABLE III. *Offspring from Individual Capsules of Plant No. 1645 (91).*

Capsule Number	Grade of Capsule	Number of seeds planted	Percentage total germination	N.	Q.	Percentage Q.
A 2	4	100	89.0	55	4	6.8
A 3	4	100	4.0	2	1	33.3
A 4	4	100	26.0	23	0	0.0
A 6	3	100	60.0	5	45	90.0
A 7	2	100	42.0	0	32	100.0
A 8	4	100	92.0	62	5	7.5
A 10	4	100	89.0	26	27	50.9
A 11	4	100	95.0	64	2	3.0
A 12	4	100	77.0	52	3	5.5
A 13	4	100	97.0	57	20	26.0
A 14	4	100	85.0	60	0	0.0
A 15	4	100	92.0	38	23	37.7
A 17	4	100	86.0	19	31	62.0
A 18	4	100	90.0	76	1	1.3
A 21	4	2	50.0	0	1	100.0
A 22	0	50	30.0	2	5	71.4
A 24	2	334	63.2	2	122	98.4
A 25	0	100	43.0	6	19	76.0
A 26	4	100	97.0	69	0	0.0
A 27	2	178	86.5	19	139	88.0
A 28	2	216	25.0	15	28	65.1
A 30	2	319	83.6	24	60	71.4
A 31	1	78	75.6	11	23	67.7
A 32	1	102	59.8	12	28	70.0
A 33	1	176	92.0	47	46	49.5
A 34	3	100	75.0	4	24	85.7
A 35	3	80	50.3	4	6	60.0
A 36	3	157	92.0	60	20	25.0

TABLE IV. *Offspring from Individual Capsules of Plant No. 1618 (9).*

Capsule Number	Grade of Capsule	Number of seeds planted	Percentage total germination	N.	Q.	Percentage Q.
B 1	2	85	92.8	28	10	26.3
B 2	2	69	91.3	21	9	30.0
B 3	0	100	90.0	34	28	53.8
B 4	1	100	85.0	38	22	36.7
B 5	2	69	75.4	12	0	0.0
B 6	1	100	73.0	27	3	10.0
B 7	2	100	94.0	35	31	47.0
B 8	1	100	82.0	43	1	2.3
B 9	0	22	81.8	9	6	40.0
B 10	4	100	97.0	51	0	0.0
B 11	0	25	60.0	10	0	0.0
B 12	1	100	84.0	12	26	68.4
B 13	4	100	95.0	62	5	7.5
B 14	4	64	89.1	44	0	0.0
B 15	4	100	93.0	58	0	0.0
B 16	1	11	100.0	3	7	70.0
B 18	3	100	90.0	26	32	55.2
B 19	3	75	93.3	52	1	1.9
B 20	2	100	93.0	32	6	15.8
B 22	0	100	95.0	31	22	41.5
B 23	0	50	92.0	12	24	66.7
B 24	0	17	58.8	5	0	0.0
B 25	4	100	89.0	37	6	14.0
B 26	3	27	92.6	11	11	50.0
B 27	2	100	79.0	21	34	61.8
B 28	2	77	85.7	25	22	46.8
B 29	4	89	100.0	54	0	0.0
B 30	2	63	17.5	6	2	25.0

TABLE V. *Summaries of Tables III and IV.*

Grade	Number of Capsules			Number of Seeds Planted			Average Percentage Germination			Average Percentage Quercina		
	A	B	A and B	A	B	A and B	A	B	A and B	A	B	A and B
0	2	6	8	150	314	464	36.5	79.6	58.1	73.7	33.7	53.7
1	3	5	8	356	411	767	75.8	84.8	80.3	62.4	37.4	49.9
2	5	8	13	1147	663	1810	59.9	78.6	69.3	84.6	31.6	58.1
3	4	3	7	437	202	639	69.3	91.9	80.6	65.0	35.7	50.4
0-3	14	22	36	2090	1590	3680	60.4	83.7	72.1	71.4	34.6	53.0
4	14	6	20	1302	553	1855	76.4	93.9	85.2	23.9	3.6	13.7

TABLE VI.

Offspring from Individual Valves of Capsules of Plant No. 1645 (91).

Capsule	Valve A			B			C			D		
	Grade	N.	Q.	Grade	N.	Q.	Grade	N.	Q.	Grade	N.	Q.
A 24	1	2	37	3	2	40	1	3	31	3	2	14
A 27	1	1	8	2	2	24	2	3	32	1	7	23
A 28	3	7	5	2	0	9	2	3	9	0	5	5
A 30	2	1	13	0	5	10	2	6	11	2	1	20
A 31	2	5	8	3	3	0	0	2	8	0	1	7
A 32	0	3	13	0	1	5	1	3	6	1	5	4
A 33	4	7	9	0	18	9	0	11	15	0	11	13
A 36	3	17	6	3	14	8	3	16	3	3	13	3

Totals } Grade 0 = 59.9 % Q. : Grade 1 = 83.9 % Q. : Grade 2 = 85.7 % Q. :
 } Grade 3 = 51.6 % Q. : Grade 4 = 56.3 % Q.

TABLE VII. *Transmission of Quercina through Pollen.*

Pedigree Number	Parent	Type of Pollination	Grade of Capsule	Normal	Quercina	Percentage Quercina
16512	A 7 × A 7	Q. × Self	2	0	32	100.00
16624	16122 (4) × A 7	N. × Q.	4	11	86	88.66
16680	16122 (17) × A 7	N. × Q.	4	9	61	87.28
16679	16122 (17) × Self	N. × Self	4	89	0	0.00
16511	A 11 × A 11	Q. × Self	4	64	2	3.03
16659	16122 (13) × A 11	N. × Q.	4	25	0	0.00
16670	16122 (15) × A 11	N. × Q.	4	14	0	0.00
16510	A 12 × A 12	Q. × Self	4	52	3	5.45
16612	16122 (2) × A 12	N. × Q.	4	35	0	0.00
16628	16122 (5) × A 12	N. × Q.	4	86	6?	6.52
16626	16122 (5) × Self	N. × Self	4	50	0	0.00
16639	16122 (7) × A 12	N. × Q.	4	90	5?	5.26
16636	16122 (7) × Self	N. × Self	4	43	0	0.00
16655	16122 (11) × A 12	N. × Q.	4	30	31	50.82
16658	16122 (13) × A 12	N. × Q.	4	46	0	0.00
16673	16122 (16) × A 12	N. × Q.	4	91	0	0.00
16441	1634 (11) × A 12	Q. × Q.	—	2	71	97.26
16501	1645 (65) × A 12	Q. × Q.	—	6	61	91.04
16509	A 15 × A 15	Q. × Self	4	38	23	37.71
16617	16122 (3) × A 15	N. × Q.	4	92	0	0.00
16615	16122 (3) × Self	N. × Self	4	44	0	0.00
16729	16169 (63) × A 15	N. × Q.	4	24	0	0.00
16742	16169 (69) × A 15	N. × Q.	4	91	0	0.00
16665	16122 (14) × A x	N. × Q.	4	2	91	97.85
16662	16122 (14) × Self	N. × Self	4	43	0	0.00
16710	16169 (50) × A x	N. × Q.	4	0	10	100.00
16709	16169 (50) × Self	N. × Self	4	29	0	0.00

TABLE VIII.

Species Tested	Grafts with Q.	Results
1. <i>Datura Stramonium</i> (Jimson Weed)	many	Always infectious (cf. text)
2. <i>Datura meteloides</i>	3	Infection, but slow in appearing; transferable back to Jimson (cf. text)
3. <i>Datura ceratocaula</i>	2	No infection evident, except three slightly abnormal flowers (cf. text)
4. <i>Browallia demissa</i>	5	No infection; cions fruited
5. <i>Capsicum annuum</i> (Pepper) ...	2	No infection; one cion fruited
6. <i>Lycopersicum esculentum</i> (Tomato)	3	No infection; cions fruited; one out of three grafts back to Jimson caused infection
7. <i>Nicotiana affinis</i>	1	No infection
8. <i>Nicotiana Tabacum</i> (Tobacco) ...	3	No infection; cions fruited
9. <i>Petunia hybrida</i>	8	No infection; cions fruited (cf. text)
10. <i>Solanum Pseudo-capsicum</i> (Jerusalem Cherry)	2	Slight infection; back graft to Jimson caused infection in one case out of two (cf. text)
11. <i>Solanum citrullifolium</i>	2	No infection; cions with flowers and spiny burs
12. <i>Solanum Dulcamara</i>	3	No infection; cions fruited; back graft to Jimsons caused no infections
13. <i>Solanum Melongena</i> (Egg-plant)	2	One cion showed slight infection; one cion fruited (cf. text)
14. <i>Solanum tuberosum</i> (Potato) ...	2	No infection

EXPLANATION OF PLATES.

PLATE II.

Fig. 1. Seedlings in 3-inch pots; upper row Quercinas, lower row normal controls.

Fig. 2. Later stage of same seedlings shown in Fig. 1 similarly arranged. Lower left control now seen to be Q.

PLATE III.

Fig. 3. Buds and mature flowers of Jimsons; at extreme right calyx removed; upper row Q., lower row normal.

Fig. 4. Dissections of pistils and stamens; left row Q., right row normal; figure slightly enlarged.

PLATE IV.

Fig. 5. Upper row successive leaves from a normal plant; lower row, the same from a comparable Q. plant.

Fig. 6. Branch of a field-infected Q. plant showing degrees of spininess from normal armed to almost entirely smooth.

Fig. 7. (Insert. in Fig. 6.) Capsule with one side smooth and other side spiny from field-infected Q. plant.

PLATE V.

Fig. 8. Green-stemmed stock with purple Q. cion grafted on left fork and purple normal cion grafted on right fork. Infection has caused production of smooth capsules on the normal cion and on the two branches of the stock below the fork.

Fig. 9. Cions of *Datura meteloides* grafted on to normal Jimson at left and on to Quercina Jimson at right. *D. meteloides* cion on Q. stock shows infection in crumpling of leaves.

PLATE VI.

Fig. 10. Seedlings from *Quercina Datura meteloides*; Q. at left, normal at right.

Fig. 11. Stock of *Quercina Jimson* supporting a cion of *Petunia* which bears at its apex a normal Jimson cion. The *Petunia* has failed to transmit the infection from the Q. stock to the normal Jimson cion.

Fig. 12. Jimson Weed attacked by a contact infectious disease (Z) of the mosaic type. Youngest leaves are reduced to the midrib.

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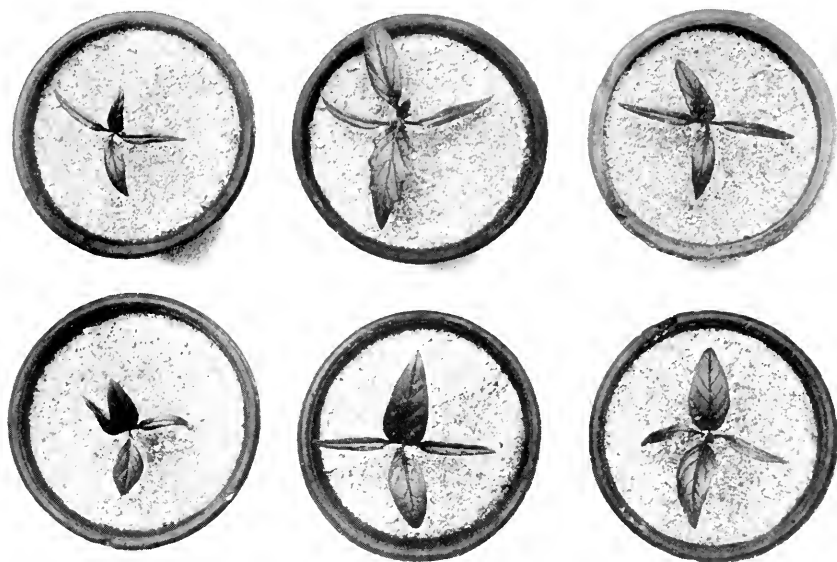


Fig. 1.

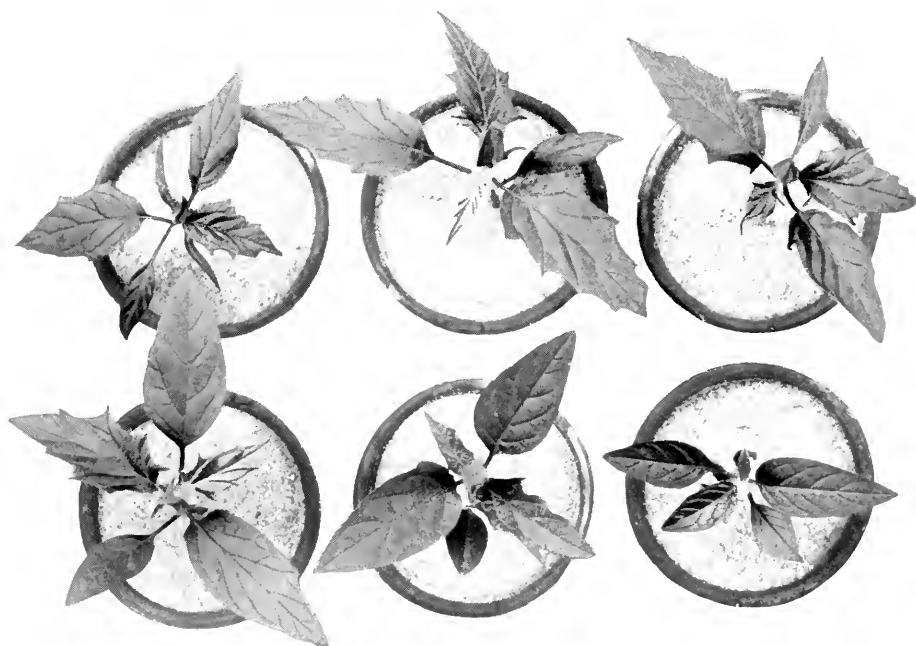


Fig. 2.

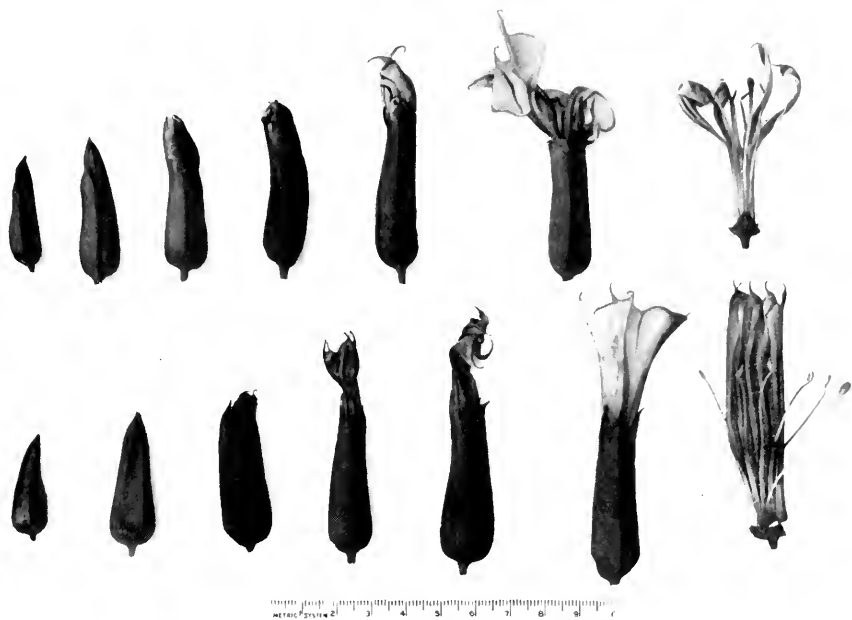


Fig. 3.

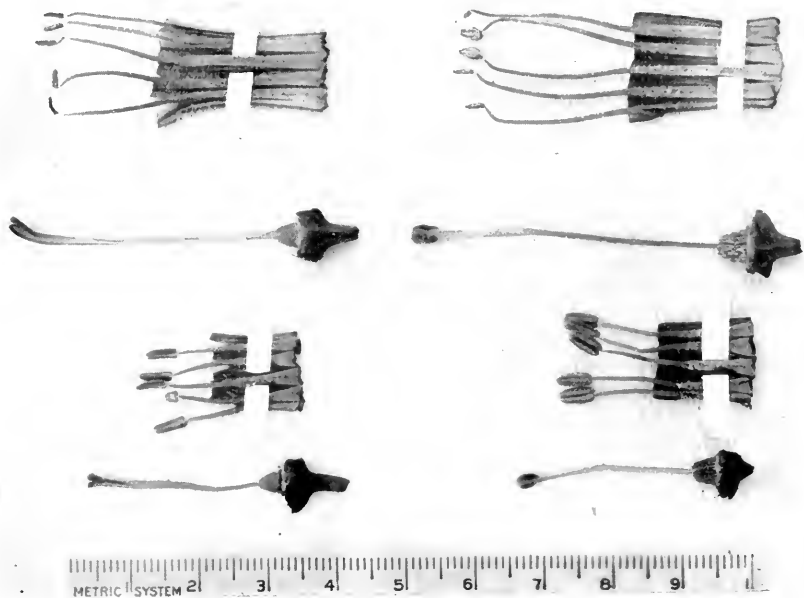


Fig. 4.

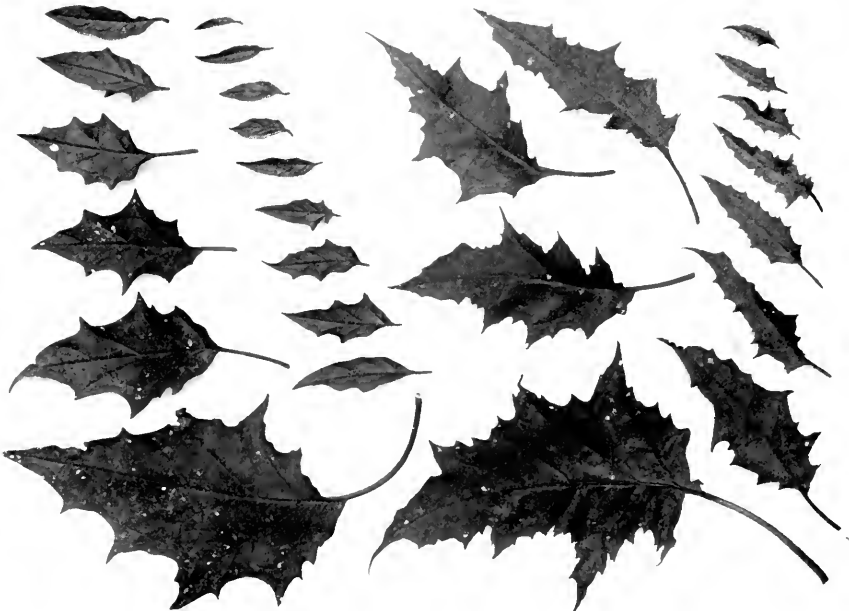


Fig. 5.



Fig. 6.

Fig. 7.



Fig. 8.



Fig. 9.



Fig. 10.



Fig. 11.



Fig. 12.

GENETIC STUDIES IN POULTRY.

III. HEN-FEATHERED COCKS.

By R. C. PUNNETT, F.R.S.,
AND THE LATE MAJOR P. G. BAILEY, R.F.A.

(With two Text-figures and Plates VII—XI.)

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Introduction.

IN certain breeds of poultry, notably in the Sebright Bantam, in Henny Game, and in certain strains of Campines¹, the cock is normally feathered like the hen. The hackles, saddle feathers, and the feathers of the tail in such henny cocks are of the form of the corresponding feathers in the female, a peculiarity which will be found illustrated in any of the standard works on poultry. In 1911 we started to investigate the genetics of hen-feathering in the male bird, making use of the Silver Sebright Bantam as our hen-feathered breed. It happened that Prof. Morgan in America started some similar experiments in the same year. As he has recently published a sumptuously

¹ Henny cocks may occasionally occur in other breeds. Lamon and Slocum figure a henny Silver Wyandotte and a henny Silver Spangled Hamburg; and it is well known that they may occur in Pencilled Hamburgs (see Plate IX).

illustrated volume on his work (1919), it is unnecessary for us to give more than a brief account of our experiments, pointing out wherein they agree with his, and wherein they differ.

Experimental data.

Our F_1 birds were bred from two Silver Sebright hens and a Gold Pencilled Hamburgh cock. Of the eight F_1 cockerels reared (which of course were all Silvers), five were fully hen-feathered¹ (cf. Text-fig. 1), two were cock-feathered (cf. Text-fig. 2), and one was intermediate, though with a pronounced tendency to the henny type. To the nature of such intermediates we shall recur later. The Sebright hens were



Text-fig. 1. Henny F_1 ♂ (ex Sebright \times Hamburgh) Text-fig. 2. Normal feathered F_1 ♂ (ex Sebright \times Hamburgh)

not tested separately, but it is clear that one of them, at any rate, must have been heterozygous. The indication that henny feathering behaves as a dominant to normal cock feathering was confirmed by the results obtained in 1912 and in subsequent years. During the period 1912—1919 we raised 463 male birds from birds heterozygous for henny feathering mated with birds known not to carry the henny factor. These 463 cocks fell into two distinct classes, viz. those normally cock-feathered, and those which were either fully hen-feathered or intermediate. For reasons that are given below (p. 42) the intermediates are to be regarded as hen-feathered birds. As is shewn in

¹ The parents and various progeny from this cross are figured in this Journal, Vol. iv. 1914, Pl. 4.

Table I (p. 55) henny and normal cocks appear in approximately equal numbers, the total containing 229 henny and 234 normal. We should mention that although we have frequently bred from normal cocks born of henny parents, we have never bred a henny bird in this way. Our experiments suggest therefore that the difference between a henny and a normal bird is a difference of a single factor throughout.

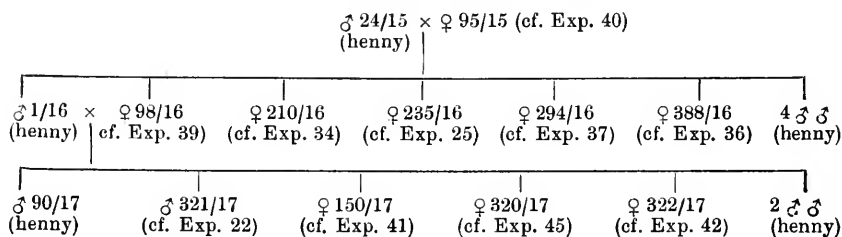
It will be noticed that several of the earlier matings recorded in Table I are between F_1 birds. In 1912 we put up five pens of F_1 birds, since we wished to raise a considerable F_2 generation in connection with the inheritance of weight. Two of these were headed by normal F_1 ♂♂, and three by henny F_1 ♂♂. Two of the latter turned out to have been mated with F_1 ♀♀ (♀ 152 and ♀ 380 in Experiments 1 and 5) which did not transmit the henny character to their sons, for when subsequently mated with normal cocks they gave only normal cock-feathered sons. The remaining F_1 henny cock (♂ 203) was mated with F_1 ♀ 383, and of the 19 ♂♂ reared 16 were henny and 3 were cock-feathered. This experiment is referred to in Table I as Exp. 43. ♀ 383 was subsequently mated to a cock-feathered F_1 ♂ (398) and proved to be heterozygous (Exp. 25). The mating between ♂ 203 and ♀ 383 was a mating between two heterozygotes, and the proportions of henny and normal ♂♂ resulting was not far removed from the expected 3:1 ratio.

Of the birds bred in Exp. 43 three henny ♂♂ and eight pullets were tested in order to ascertain whether any of them were homozygous for the henny factor. Two of the henny ♂♂ were mated with normal ♀♀ (Exps. 10 and 11) and both proved to be heterozygous. The third, mated with a sister (♀ 668), produced six henny and two normal sons¹. All three of the cocks tested proved to be heterozygous. Of the eight pullets, two, mated to heterozygous cocks, gave both hennies and normals; three, mated with normal cocks, gave both hennies and normals (Exps. 27, 28, 29); while the remaining three, mated to normal cocks, gave 9, 6, and 11 normals respectively. None of the eight therefore could have been homozygous. On ordinary expectation one of the three cocks and two of the eight pullets should have been homozygous for the henny factor. We failed however to find such a bird among the eleven that were tested.

Later on we made another attempt to find a homozygous bird. A henny ♂ (24/15) from Exp. 31 was mated with a sister (♀ 95/15), who was subsequently proved to be heterozygous in Exp. 40. This mating is

¹ This experiment is not included in the table as the hen used may have been heterozygous.

referred to in Table I as Exp. 44. All of the five cockerels reared turned out to be henny, while all of the five pullets tested proved to be heterozygous. One of these henny cockerels was mated with a sister ($\text{♀ } 98/16$)



who was shewn to be heterozygous in Exp. 39. From this mating all of the four males produced were henny. Two of these were subsequently mated to normal hens. One of them ($\text{♂ } 321$) proved to be heterozygous. The other ($\text{♂ } 90$) produced two henny cocks from a Brown Leghorn hen in 1918, but in 1919 he failed to get any chickens. Mated with a different hen he has given some chicks in the present year, but as yet they are too young to be sure whether they are all henny or not¹. All of his three sisters proved to be heterozygous. It is possible that $\text{♂ } 1/16$ was homozygous, but as four of his five offspring tested were certainly heterozygous and the remaining one so far doubtful, it is more likely that he was heterozygous. We attempted to breed from him again in 1918, but although he was apparently a vigorous bird he failed to fertilise an egg. He was killed on April 26, 1918, and histological examination shewed that his spermatogenesis was abnormal. The matter is being investigated further as a good deal of sterility has occurred in this inbred strain.

So far then the search for a homozygous henny bird has not been successful. Of 15 birds produced by mating heterozygotes together, and shewn to transmit henny feathering, 14 were definitely proved to be heterozygous, the remaining one at present being doubtful. Normally we should have expected five homozygotes among the 15. This may of course be a chance result, but there is the possibility of the homozygous bird being non-viable in the strains that have arisen in the course of our experiments. Further work to decide this point is now in progress.

¹ [Note added November 9, 1920.] Of the four cockerels reared this year all have come henny. Up till now therefore all of the six sons of $\text{♂ } 90$ have proved henny, and it is not unlikely that he may be homozygous. It is hoped to test him further next year.

Intermediates.

We have already stated that birds of an intermediate type of feathering, as well as purely hen-feathered birds, have arisen during our experiments; and indeed the intermediates have greatly outnumbered the typically hen-feathered ones. Though we are not at present in a position to offer a satisfactory explanation of the nature of these intermediates, we may record certain observations which we have made in connection with them.

(1) The intermediate condition shews a great deal of variation. Some intermediates differ but slightly from a purely henny bird in appearance. The majority of the saddle feathers are typically henny, but scattered among them are a few in which the tip of the feather exhibits the lack of barbules and the orange colour¹ characteristic of the typical male feather. Where the general colour of the feather is dark, the orange fringe at the tip is very conspicuous. Three feathers from such a bird are shewn on Pl. VII, fig. 3, of which two are intermediate in type and the other a purely henny one.

In other cases the intermediate approximates far more closely to the condition found in the normal cock. Sometimes indeed the approximation is so close that such birds might easily be classified as normal feathered unless the observer were on his guard². Careful search however has always revealed the presence of a few henny or nearly henny feathers among the young feathers coming through. Moreover, as will be explained below, any doubt as to the nature of the bird is always resolved at the first moult. Where we have had any doubts as to the true nature of the feathering, we have kept the bird until it was 18—20 months old. A good example of this type of intermediate feathering is figured on Pl. VII, fig. 1. In their gold colour and general appearance, they might pass for feathers from a typical male. Between these two extremes all sorts of grades of intermediate feathers are to be found, such for example as those figured on Pl. VIII, figs. 1 and 3. From the almost henny feather to that which resembles a normal cock feather, a practically continuous series might be formed from a small number of intermediate birds. For the feathers on the same bird are not all of precisely the same grade.

¹ This of course when the bird is genetically a gold. The tip is white, or nearly so, when it is genetically a silver.

² When such birds first made their appearance in a certain pen during the early days of the work we recorded some as normal ♂♂. However we discovered our mistake, and the results from this pen are not included in the present account.

(2) Nevertheless all of these grades of intermediates behave alike in one respect. At the first moult they all become fully henny, or nearly so. We have now kept some dozens of intermediate birds over their first moult without meeting any exception to this rule. In some cases the change to henny feathering is complete. As a typical example we may take the case of ♂ 105/18 (Pl. VII, fig. 1). A full henny cock (♂ 90/17 in Exp. 44) was mated in 1918 to a Brown Leghorn hen. Only two male chicks were reared, viz. ♂ 104/18 and ♂ 105/18. These two birds grew up so closely alike that they were indistinguishable in appearance. They were clear golds with traces of brown occurring in some of the quills and in the feathers at the base of the tail. Both were so like normal males in appearance that one of them, ♂ 104, was kept, and has now moulted twice. In 1919 all of his new feathers were purely henny, as shewn on Pl. VII, fig. 2¹. At this period however he was not full henny in appearance because some of the old intermediate feathers were not shed until the following year. By the second moult these worn feathers, which had survived from the original plumage, were all shed, and the bird is now fully henny. Noteworthy is the considerable development of melanic pigment in the saddle feathers which has accompanied the structural change.

Another good example of the change from intermediate to henny feathering at the moult is illustrated on Pl. X. Two brothers of intermediate plumage were closely similar, both in colour and in the nature of their feathering. One of them (Fig. 1) was killed at nine months old; the other was kept for a year longer, until he was over his first moult (Fig. 2). This case differs from the preceding one in that the plumage did not become fully henny. Some of the feathers shew traces of the intermediate condition, but the change as a whole is sufficiently striking. Genetically these two birds were silvers.

(3) Although intermediate birds always moult out henny, in so far as our experience goes, they may sometimes revert to the intermediate type at some later moult. In illustration of this we may take the history of ♂ 201/14, who was bred in Exp. 28. In his first plumage he was intermediate, with a marked tendency towards normal cock feathering. The sample of his feathers taken in 1914 is unfortunately lost, but they were very like those of ♂ 126/15 (from Exp. 15) shewn on Pl. VIII, fig. 1.

¹ The bird recorded by Darwin (*A. and P.*, I. p. 258) "which, after assuming its perfect masculine plumage, became hen-feathered in the autumn of the following year" was doubtless an intermediate with a pronounced tendency to normal feathering in its first plumage.

In 1915 he moulted out full henny, as shewn by the feathers figured on Pl. VIII, fig. 2. The colour of the plumage was dark mossed all over. There was no trace of any intermediate feathering, and he remained a fully henny bird until his moult in 1918, when he put up a number of intermediate feathers (cf. Pl. VIII, fig. 3). Scattered among these were a number of feathers of the henny type, but the general appearance of the bird at this stage was distinctly cock-like. At his moult in 1919 he again became purely henny (cf. Pl. VIII, fig. 4), with the exception of five worn intermediate feathers which doubtless belonged to the previous set¹. In the spring of 1920 he unfortunately went light, and died at the age of six years. It should be added that we bred from him in 1915 (Exp. 14), selecting him as an intermediate with a pronounced tendency to normal feathering. He proved a good getter, as again he did in 1918 and 1919 when tested for fertility. There are no grounds in this case for supposing that the assumption of intermediate feathering is connected with sterility.

We have so far no other case of the reversion to intermediate feathering after a lapse of several years, but this is probably because, owing to lack of space, it is only in exceptional cases that we have been able to keep birds over a period of four or more years. In the three other cases where we kept a henny cock until its fourth year, there was no appearance of any intermediate feathering. In each of these cases it is true that the bird started as a fully hen-feathered bird, and not as an intermediate. Nevertheless a bird may start as an almost henny bird and later revert to a more cock-like type, as is shewn by the history of ♂ 338/17 (ex Exp. 19). Nearly henny in his first plumage he became fully so in 1918. In 1919 however he put up so large a proportion of long intermediate feathers that his general appearance was towards that of a normal cock, particularly when viewed at a distance of 20 yards or so away. The tail sickles were also well developed, as is usual in the case of intermediates with a tendency to normal feathering. In his present moult (1920) all of his new feathers are so far henny, but many belonging to the older series are not yet shed. We shall endeavour to keep this bird, and several others, as long as possible in order to find out what the condition of the feathering is in old age.

(4) With regard to the relation between intermediate birds and those that are fully hen-feathered from the first, we have not yet

¹ The history of this bird recalls that of the polecat hen-cock recorded by Darwin (*A. and P.*, i. p. 253).

obtained satisfactory evidence. It is however clear that it is not due to the factors that influence the length of the hackles in normal breeds. Intermediates with a marked tendency to normal cock feathering can be bred from short-feathered races such as Aseels and Game Bantams, as well as from breeds relatively long in the feather such as the Brown Leghorn. Further, the various grades of intermediates together with full henny birds can be bred from the same mating, where all of them are heterozygous for the henny factor. Whether the homozygous cock can be an intermediate we cannot at present say, for, as we have already stated above, we have not yet succeeded in identifying such a bird.

Colour of Intermediates.

In our account we have restricted the term "intermediate" to birds differing from the normal cock in the structure of those feathers in which the sexes of normal breeds differ from one another. The structural difference is due to the elongation of the rachis and distal barbs, and to the loss of the barbules on the barbs. Proximally, of course, even in a truly male saddle-hackle, barbules are present and are furnished with barbicels.

When an intermediate of a pronounced cock-like type becomes henny, a marked difference in the general colour of the bird results, as well as in the form of the feathers. The principal factor in this change is the deposition of melanic pigment in the feather. It is well exemplified by the feathers shewn on Pl. VII, figs. 1 and 2. The deposition of the melanic pigment on the assumption of the henny plumage brings about a very great difference in the general appearance, and there arises the interesting question whether the henny cock assumes the colour as well as the plumage structure of the hen that corresponds genetically to him. That the colour correspondence as well as the structural one may in some cases be very close is shewn by Morgan's experiments in the castration of Sebright Bantams (cf. Morgan, 1919, Pl. I, figs. 3 and 4). If we assume that the castrated bird represents the appearance that the cock of this breed would have if the henny factor were not present in him, then we must suppose that the "hennification" of such a male would result in a cock which in colour, as well as in plumage structure, was practically identical with the hen. There are many breeds in which the cock differs markedly from the hen in colour in those feathers only in which there is a structural difference in the sexes. This is naturally true of self-coloured breeds such as blacks, buffs, and whites, as well as

of blues. It is true also of many breeds where the feathers exhibit a definite pattern such as most of the barred, pencilled¹, laced, and spangled breeds. In the last case it is true whether the spangled feather is predominantly light with a black tip, as in Hamburgs, or predominantly black with a light tip, as in Anconas. It is true also of Brown-breasted Game. On the other hand there are breeds in which the colour differences between the sexes are not limited to the sexual feathers. This is the case in Black-reds and in Silver-greys, where we find a marked difference between the black breast of the cock and the salmon-coloured one of the hen. The difference also occurs in the abdominal and leg feathers, which are brown mottled in the hen² but black in the cock. In Piles also we find the breast colour difference, the salmon breast of the hen contrasting with the white one of the cock. A sexual colour difference, apart from the sexual feathers, is found also in certain of the laced and pencilled breeds, such as Indian Game, Partridge Cochins, and Partridge Wyandottes. In the case of these breeds, it is important to remember that the cock is either a black-red or a duckwing.

We are inclined to think that there is an essential difference between the breeds of the first group where the colour difference is restricted to the sexual feathers, and those of the second where the sexes exhibit a colour difference apart from the sexual feathers, and to suppose that the sexual colour differences are present in the second group, but are obscured by some dominant factor. The obscuring factor we consider to be a different one in different cases. In whites it is the inhibitor for colour that occurs in the dominant whites, such as Leghorns³; in blacks and blues, it is due to the factor for black; in brown breasted, there is also some factor leading to increased melanism; in buffs and light golds there is probably a factor which inhibits melanic pigmentation.

In the absence of such obscuring factors, we have the condition found in the second group with its marked sexual dimorphism in colour.

In the first group it is clear that "hennification" would lead to the production of males which in colour, as well as in feather structure, resemble the hens. Provided that the cock is fully henny, he will be coloured like the hen. Now, as we have already pointed out, the hetero-

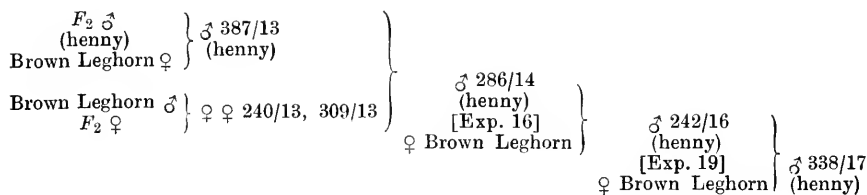
¹ The amount of melanic pigment is throughout much reduced in the cocks of pencilled breeds, but such as exists exhibits the same arrangement as in the hen.

² In writing this we had in mind the Brown Leghorn and the Silver-grey. In wheaten hens the Salmon tint is found also over the abdomen and thighs.

³ In recessive whites of course the obscuration is brought about through the absence of some factor essential to pigment production.

zygous bird may be fully henny, and among the fully henny heterozygous birds that we have bred we have had some which in colour, as well as in feather structure, closely matched the corresponding hen. The heterozygous Silver-Pencilled Hamburg, figured on Pl. IX, offers a good example of this. Again, among the fully henny F_2 heterozygous birds that we bred, ex Sebright \times Hamburg, we had examples of silver-laced and of gold-pencilled birds which were henny in colour and pattern as well as in feather. When we introduced the Brown Leghorn we obtained some dark mossed cocks which corresponded exactly in colour to hens similarly bred. The feathers of these birds were very like those of ♂ 201/14, figured on Pl. VIII, figs. 2 and 4. From their dark eyes and the purplish tinge in the face we have little doubt that, as compared with a Black-red, they contained some obscuring factor operating for the increased production of melanic pigment. This is further borne out by the down colour of such birds, which was dark blackish-brown, a colour known to be dominant to brown stripe. The henny Silver Wyandotte figured by Lamon and Slocum (p. 105) is evidently like a hen in colour and pattern, and as these birds are uncommon it is extremely likely that he was heterozygous. We are inclined therefore to consider that in our first group the heterozygous bird, if fully henny in feather structure, resembles the hen also in colour.

We doubt however whether this applies to the birds of our second group, where sexual differences occur in colour apart from the sexual feathers. In order to try and throw light on this point we attempted to "hennify" the Brown Leghorn by repeated crosses of heterozygous cocks with Brown Leghorn hens. The nature of the experiment is summarised in the accompanying scheme:



In this series of matings our procedure was to choose from our available birds the cock that was nearest to a black-red, and mate each time with a Brown Leghorn. ♂ 286 \times Brown Leghorn ♀ gave chicks with two types of down, viz. dark black-brown and brown stripe in almost equal numbers. Of the brown-striped ♂ 242 resembled a Brown Leghorn in juvenile plumage, subsequently becoming a henny. The

general colour however was much redder than that of a Brown Leghorn ♀, while he had a black breast and the characteristic chestnut wing-bow of the Brown Leghorn cock. Mated with a Brown Leghorn hen (Exp. 19) he gave 17 chicks, all brown-striped. They proved delicate, however, and only five (4 ♂♂ and 1 ♀) were reared to maturity. Of the 4 ♂♂, two were exactly like normal Brown Leghorns; one was like a Brown Leghorn, except that the breast feathers were mixed salmon and black instead of full black; and the last, a henny bird (♂ 338), was very like the father. The solitary hen was indistinguishable in appearance from a Brown Leghorn. She proved to carry the henny factor (Exp. 38), and was subsequently mated with ♂ 338 in the hope of establishing a homozygous henny Brown Leghorn strain. Unfortunately the union proved sterile. But although both ♂ 242 and ♂ 338 were, apart from the henny factor, almost certainly genetically similar to the Brown Leghorn, and although, at some period, both were fully henny birds, nevertheless their colour was very different from that of the Brown Leghorn hen. The most noticeable differences were (a) the retention of the chestnut-brown wing-bow, (b) the presence of black or black and salmon feathers on the breast, and (c) the presence in the saddle of warm chestnut-brown feathers, as well as of others shewing some beetling, interspersed among the brown mossed hen-like feathers.

We are therefore inclined to think that in the breeds belonging to our second group, where sexual colour differences exist apart from the sex feathers, the heterozygous bird may be fully henny in plumage structure, but not in colour. Whether the plumage would be fully hen-like in colour in a homozygous henny cock is a point we have been unable hitherto to decide. But there is evidence for supposing this to be the case. In the picture of light red hennies given in Cassell's *Illustrated Book of Poultry* (1876), on Plate 25, the colour of the two sexes is identical, the cock having a deep salmon breast and saddle feathers coloured exactly like the hen. We are also indebted to Mr Herbert Atkinson, the well-known authority on Game Fowl, for the information that the true breeding pile henny cock is coloured like the hen.

On the whole therefore the available evidence suggests that the henny factor may bring about a complete change to the henny condition in the heterozygous bird both in the structure of the feathers and in the colour of the sexual feathers, but, where the sexes differ in colour in other than the sexual feathers, the bird must be homozygous before the colour change is complete.

The hypothesis of complementary factors.

In the account of his experiments on the nature of henny cocks, Morgan suggests that the Sebright differs from the normal (in this case, Black-red Game Bantams) in two factors. The presence of both of these factors is assumed to be necessary for the development of henny feathering. This interpretation rests almost entirely upon the proportions of henny and normal cocks appearing in the F_2 generation, and Morgan points out that the experimental numbers, viz. 31 henny to 28 normal, are far removed from a 3:1 ratio but approximate closely to a 9:7 ratio. A few birds were bred by crossing F_1 with game, and of these two are recorded as henny and seven as cock-feathered. This again is close to expectation on the hypothesis of two complementary factors.

We venture to suggest a possible interpretation of Morgan's results which would bring them into harmony with our own, viz. that some of the birds recorded by him as cock-feathered were in reality intermediate birds of the type that shews a marked approximation to normal cock feathering. If a dozen of his 28 F_2 ♂♂, recorded as normals, were of this type, we should have a close approximation to a 3:1 ratio. We have already pointed out how easily one may classify these cock-like intermediates as of normal plumage, unless one is on one's guard. The distinction was forced upon us by the change to henny plumage that occurred at the moult of such birds. Morgan makes no remark about changes in the character of the feathering at moult, and one is led to suppose that his birds were generally destroyed before this stage was reached. We consider that our view is indirectly supported by the statement that Morgan makes with regard to intermediates. He recognises such birds among his F_2 ♂♂, but states that "the line between intermediate and cock feathering is sharp, all the intermediates belonging distinctly to the hen-feathered group, but the line between the two subdivisions of hen-feathered birds is not sharp, and occasionally a bird is found that is difficult to place" (p. 15). Unfortunately we are given no illustrations of the feathers of these intermediate birds, but it is evident from the account that they approximated to the full henny condition, and perhaps resembled such birds as the one whose feathers we have figured on Pl. VII, fig. 3.

We may add that we have examined our own data carefully on the supposition that two complementary factors might be concerned with henny feathering, but find no grounds for supposing such to be the case. In our experiments, which involve a far greater number of

matings and of birds than Morgan's, the hypothesis of a single factor is so clearly adequate that we have ventured on the above criticism in an attempt to reconcile his results with our own.

Castration Experiments.

Among the most interesting features of Morgan's work was the demonstration that castration of the henney cock led to the assumption of normal male plumage at the next moult. Thanks to the co-operation of Dr F. H. A. Marshall we are able to confirm Morgan's results. As an example we may give the history of ♂ 204/15 (ex Exp. 14). In plumage structure this bird was nearly full henney, a few of the feathers being slightly intermediate, of the grade shewn on Pl. VII, fig. 3. In general colour he was a warm chestnut, due to the presence of a number of feathers of this colour mingled with the typical hen-like brown mossed feathers. He was very like the henney cock figured on Pl. XI, fig. 1, and we have little doubt that if he had been allowed to moult in the normal way he would have become a full henney bird with a preponderance of hen-like brown mossed feathers on the back and saddle. In June 1916 the testes were removed by Dr Marshall. On Oct. 1 following he is recorded as throwing up normal male feathers. Subsequently he became feathered like a Brown Leghorn cock. He was kept over another moult, and eventually killed for a skin in Nov. 1917. He was, as shewn on Pl. XI, fig. 2, very like a Brown Leghorn cock both in plumage structure and colour. We may add that although he would flirt with hens introduced into his pen, he made no attempt to tread them. After death an autopsy made by Dr Marshall revealed no traces of testes.

The birds placed at Dr Marshall's disposal for castration were all adult or nearly so. For we had to make use of material from families containing both hennies and normals, and until a bird is about three parts grown it is often difficult to distinguish the intermediate from the normal, and to be sure that it belongs to the henney class. In the first batch of experiments the mortality was high, and Dr Marshall suggested that this might be avoided by removing one testis at a time, allowing the bird to recover in between. Accordingly three brothers (♂♂ 78/15, 104/15, and 276/15 from Exp. 16) were operated on between Oct. 28 and Nov. 7, 1916. In each case the right testis was removed. All of these birds were intermediates in their first plumage, but had already assumed the full henney type at the date of the operation, being at that date more than 18 months old. In each case an excellent recovery was

made, and when examined in Feb. 1917 it was found that two of them, 104 and 276, were putting up some feathers of the cock-like intermediate type. Further, these feathers were almost entirely confined to the right side of the body, i.e. the side on which the operation took place. The third bird, ♂ 78, remained henny. The left testis in each bird remained intact throughout. Of the two birds which put up intermediate feathers, one (♂ 276) was killed in July 1917 in order to preserve the skin as a record. The other was kept over another moult, and, having become fully henny again, was killed on March 3, 1918. The explanation of this peculiar phenomenon is obscure. It is clear that a local lesion may influence the character of the feathering on the side on which it occurs, although the hormone must be supposed to be circulating equally on both sides. It seemed conceivable that injury to the sympathetic nervous system may have been concerned, for it is so closely in contact with the genital gland that it is impossible to remove the latter without nervous damage. We think however that, in the light of some subsequent experiments by Dr Marshall, another explanation is possible.

Dr Marshall removed the right testis in three birds hatched in 1919, the operation being performed in November. Two of these birds (♂ 337 and ♂ 400) were almost fully henny in their first plumage, and remained so after their moult in 1920. In neither case did they put up any intermediate feathers on the side on which the operation took place. The third bird (♂ 346) was intermediate in the character of the feathering. In March 1920 he shewed a well-marked patch of full henny laced feathers on the fore part of the right saddle, i.e. in the position in which most of the intermediate feathers appeared in ♂ 104 and ♂ 276. The relatively sharp lacing and paler ground of these henny feathers made the patch shew up conspicuously against the more warmly tinted intermediate feathers. Later on in the year this bird moulted out practically full henny, the feathers on both sides being similar to those found on the patch that appeared earlier on the right side. Whatever the reason, the operation seems to have caused an earlier appearance on the right side of feathers which would normally have developed at the next moult. We know that henny birds may subsequently develop an intermediate type of feathering (p. 42). It seems just possible that ♂ 276 may have been such a bird, and that the operation led to a premature development of intermediate feathers because he would have developed such feathers at his next moult had he not been killed. On the other hand, ♂ 104 was allowed to live and

moulted out henny. In his case however the development of intermediate feathers was much less marked, and the tendency to develop them may have been overcome by the time the moulting season arrived. The whole matter remains obscure. It is clear that much more experimental work must be undertaken before we can hope to understand it.

General Discussion.

Granted then that hen-feathering behaves in heredity as though it were dependent upon a single factor; further, that its manifestation depends upon the presence of the gonad, we may ask whether we can associate the factor with any particular tissue. This Morgan claims to have done, regarding the so-called luteal cells of the ovary as the seat of a hormone which brings about the development of feathers belonging to the hen type. He states that these luteal cells are also found in the testis of henny, though not in those of normal cocks. If this is so, it is plausible to identify the henny hormone with a specific tissue. The identification is supported by Goodale's work on the Brown Leghorn hen, as well as by the work of Pézard, castration in either case leading to the assumption of the normal cock plumage. It seems clear that henny feathering, in either sex, is due to a hormone produced in the gonad: and that something necessary for the production of this hormone can be represented by a factor in gametogenesis. So far as we can see, there is no reason for regarding a hormone that leads to hen-feathering in the female as different from one leading to hen-feathering in the male. Each produces a similar effect, and the effect of castration is in each case similar. We are led therefore to infer that the factor transmitted is identical in the two cases. If this is so, it is clear that the precise mode of transmission in the two cases is different.

In normal breeds we must suppose the transmission to be sex-linked. The female we may regard as heterozygous for the henny factor as well as for sex. To her daughters she transmits both the factor for femaleness and that for hen-feathering: to her sons, neither. In other words there is complete linkage between these two factors in the gametogenesis of the normal hen; and if we had no knowledge of henny cocks, we might have considered the two characters as due to one and the same factor. There is however a point of difference between this and the other sex-linked cases hitherto described in poultry. In all of these the heterozygous hen transmits the recessive character to her daughters, the dominant to her sons. We may recall the barring of the Plymouth Rock, silver plumage as opposed to gold, the inhibitor for the pigmen-

tation of the silky fowl, as well as that for shank pigmentation, etc. In the present case however it is the dominant character that is transmitted to her daughters by the heterozygous hen, and the recessive to her sons.

When we come to the purely henny breeds we might at first sight suppose the factor to be carried by both sex-chromosomes, in the male as well as in female. We are, however, at once met with the difficulty that the heterozygous hen, produced by mating a hen of a normal breed with a henny cock, transmits the character to all of her daughters but to only half of her sons. Such a result challenges comparison with the cases of sex-linked heredity in man where the female carrier, mated with a normal, transmits to half of her sons. The resemblance however is but superficial: in the human case the sexually homozygous female transmits to half of the heterozygous sex, while in poultry it is the sexually heterozygous female that transmits the peculiarity to half of the homozygous sex.

We feel that the simplest way of summarizing the facts is to suppose that in all poultry the factor associated with the sex-linked mechanism comes into play; whereas in families in which henny cocks appear, an independent, though apparently identical factor also comes into operation, and that in heredity this factor behaves in the usual way, uncomplicated by sex linkage. The hen of a pure henny strain is, on this view, homozygous for **A**, which can be transmitted to either sex. At the same time she is also heterozygous for the factor **A'** which she transmits only to her daughters. Again, a hen that arises from mating a pure henny cock with a normal hen is heterozygous for both **A** and **A'**. The latter she transmits to her daughters only; the former to half of her sons and half of her daughters. Half of her sons will be henny. But since all of her daughters receive **A'** through the sex-linked mechanism, those which receive **A** will not be visibly distinct from those which do not. The former, however, differ from the latter in transmitting henny feathering to half of their sons. **A** and **A'** we regard as producing the same effect, but differing in the mechanism of their transmission. Translated into terms of chromosomes, this amounts to saying that **A'** is only found in the sex chromosome peculiar to the female¹, whereas **A** may occur in some pair of chromosomes which is equally represented in both sexes. Whether the sex-linked connection preceded the ordinary one in evolutionary history, or the reverse; whether the double connection may be regarded as more primitive than either single one; and how the dislocation, if there be one, was brought about, are questions to which we can offer no answer.

¹ Assuming, of course, that there is such a thing.

We may however recall that certain human defects present analogous features in their heredity. Night-blindness may in some families be sex-linked (cf. Newman, 1913), while in others it behaves as an ordinary dominant (cf. Nettleship, 1907). And from the data collected by Nettleship (1909) on Leber's disease, it would appear that both forms of transmission may occur here also. It seems not unlikely that some of the complications found in such pedigrees may be due to the dual mechanism involved in the transmission of the same factor. There is however a remarkable feature about night-blindness, in that it behaves as a dominant when transmitted equally to either sex; whereas, when associated with the sex-linked mechanism, its behaviour is that of a recessive. Apart from this peculiarity, and having regard only to the sex-linked cases, there is a further point of difference between the human being and the fowl. From analogy with *Drosophila* we are led to infer that the sex-chromosome peculiar to the heterozygous sex cannot carry a sex-linked factor. But in the poultry case it is difficult to see how we can avoid supposing that the factor for henny plumage in normal breeds is carried by the sex-chromosome peculiar to the heterozygous sex, in this case the female. Though the human cases resemble the poultry case in shewing both sex-linked and ordinary inheritance, there are clearly difficulties in the way of instituting a closer parallel between them.

In suggesting the view of henny-feathering outlined above, we have not overlooked the possibility of an interpretation on the lines so ably developed by Goldschmidt for the intersexes in his *Lymantria* crosses. Such an interpretation, however, implies a different result in the reciprocal crosses between normal and henny breeds; and this, according to Morgan, does not obtain. Moreover, the only type of intersex produced would be the henny cock, in which comb, wattles, spurs, and sexual behaviour are all as in normal males. It seems unlikely that this single type¹ can represent both male and female intersexes. Were we to suppose that certain henny cocks were genetically females, i.e. in so far as the sex-chromosomes are concerned, we should look for a considerable excess of females in their progeny from normal hens. Our results from a number of such matings, however, shew that the sexes are produced in nearly equal numbers, i.e. 324 ♂♂ and 345 ♀♀ (cf. Table I). We incline to agree with Goldschmidt when, in his discussion of henny feathering, he says "Wir müssen gestehen, dass im Augenblick die

¹ Single, because a given cock may exhibit the extremes at different times in his life history.

Schwierigkeiten, die diese Tatsachen einer einfachen Lösung entgegenzusetzen, noch nicht behoben sind, und dass noch manche Experimente nötig sind."

Note on the sex-proportions and ratio of henny to normal cocks.

Bearing in mind the irregular sex-proportions that frequently occur where intersexes are found in animals, we thought it worth while to examine our figures from this point of view. In attempting to ascertain whether families with a marked preponderance of either sex shewed a preponderance among the cocks of either normal or henny feathered, we have divided our families into three groups, viz. (a) those with marked excess of ♀♀, (b) those with marked excess of ♂♂, and (c) those in which the proportions of the sexes approach equality (cf. Table II, p. 56). Our standard of "marked excess" must naturally be an arbitrary one, and in practice we have classified families in which three-fifths or more of the total belong to a given sex as shewing a marked excess of that sex. Thus a family with 20 ♂♂ and 11 ♀♀ is regarded as shewing a marked excess of ♂♂; a family with 7 ♂♂ and 12 ♀♀ as shewing a marked excess of ♀♀; while a family with 12 ♂♂ and 9 ♀♀ is classified as one shewing approximate equality. The classification is of course quite rough, and we do not suggest that any special significance should be attached to the resultant groups. In classifying the families, we have kept those in which the henny character came from the mother distinct from those in which it was transmitted by the father. We should add that the sexes were in most cases only recorded in the live birds as they grew up. In relatively few cases was the sex determined by dissection of a chick that had died early. The results of our grouping are given in Table II, p. 56. It will be noticed that, where the henny character is transmitted by the father, the proportion of normals and hennies among the sons is nearly equal in each of the three groups. This is also true for cases where it is transmitted by the mother, in the group where the sexes are approximately equal, and in that in which there is an excess of females. But where there is an excess of males in the offspring, the normal sons are nearly twice as numerous as the hennies. Moreover this excess of normals is found in all of the seven families concerned except one (Exp. 41), in which the numbers are very small. The figures as they stand suggest something more than chance distribution, and further experiments have been planned to test the point.

TABLE I. *Heterozygote* \times *Recessive*.A. *Cock hen*ny.

No. of Exp.	No. of Pen	Details of Mating		No. of Exp. in which male was bred	Progeny		Sexes recorded	
		Male	Female		Male-feathered cocks	Hen	Males	Females
1	21/12 + 13 + 14	396/11 (F_1)	\times 152/11 (F_1)	—	14	8	33	52
2	21/13 + 14	"	\times Br. Legh.	—	10	10	21	15
3	23/13	203/11 (F_1)	\times 376/11 (F_1)	—	7	6	13	11
4	"	"	\times Br. Legh.	—	2	3	5	4
5	24/12 + 13	397/11 (F_1)	\times 380/11 (F_1)	—	9	17	39	33
6	"	"	\times Br. Legh.	—	5	7	16	8
7	7/12	"	$F_1 \times 2 \text{ } \varnothing \text{ } \varnothing$	—	5	6	12	11
8	10/13	139/12 (F_2)	\times Br. Legh.	—	8	9	19	22
9	12/14, 4/15	"	$\times 3 \text{ } \varnothing \text{ } \varnothing$	—	12	8	21	28
10	16/13	"	$28/12 \times$ Br. Legh.	43 ¹	8	11	19	31
11	27/13, 24/14	"	$190/12 \times$ 807/12	43 ¹	3	4	9	9
12	12/13	"	$552/12 \times$ 964/12	23	7	8	23	22
13	4/12	"	$266/11 \times$ 327/11	7	7	2	12	9
14	10/15	"	$201/14 \times 2 \text{ } \varnothing \text{ } \varnothing$	29	3	5	13	11
15	11/15, 9/16	"	$165/14 \times 2 \text{ } \varnothing \text{ } \varnothing$	28	—	4	4	10
16	17/15, 19/16	"	$286/14 \times 2 \text{ } \varnothing \text{ } \varnothing$	(a)	4	6	10	26
17	23/15	"	$492/14 \times 2 \text{ } \varnothing \text{ } \varnothing$	32	3	4	7	3
18	8/16 + 17	"	$70/14 \times 3 \text{ } \varnothing \text{ } \varnothing$	2	4	4	10	10
19	6/17	"	$242/16 \times$ Br. Legh.	16	3	1	5	1
20	18/17, 23/18 + 19	"	$268/16 \times$ 479/16	18	9	10	20	11
21	11/18	"	$338/17 \times$ Br. Legh.	19	2	—	8	9
22	19/18	"	$321/17 \times 3 \text{ } \varnothing \text{ } \varnothing$	44 ²	1	3	5	9
Totals					126	136	324	345

B. *Hen hen*ny.

No. of Exp.	No. of Pen	Details of Mating		No. of Exp. in which female was bred	Progeny		Sexes recorded	
		Female	Male		Male-feathered cocks	Hen	Males	Females
23	22/12 + 13	151/11 (F_1)	\times 379/11 (F_1)	—	10	15	29	36
24	4/14	"	\times Br. Legh.	—	11	8	24	12
25	25/13	383/11 (F_1)	\times 398/11 (F_1)	—	6	3	15	10
26	14/12	146/11	\times 187/11	(β)	6	8	14	14
27	26/13	658/12	\times Br. Legh.	43 ¹	2	1	13	11
28	4/14	75/12	\times "	43 ¹	4	1	7	12
29	19/14	998/12	\times "	43 ¹	6	5	11	12
30	5/15	{ Silver Hamburgh	\times 174/13	—	1	1	2	4
31	8/15	"	$110/14 \times$ 191/14	(γ)	5	5	11	12
32	26/14 + 15	301/13	\times { 592/13 539/13	3	14	5	20	13
33	21/15	501/14	\times 407/14	33	3	4	9	7
34	10/17	210/16	\times 271/16	44 ²	3	5	8	7
35	19/17	235/16	\times 134/15	44 ²	7	2	9	7
36	20/17	388/16	\times 44/16	44 ²	5	5	11	9
37	23/17	294/16	\times 131/16	44 ²	4	7	11	16
38	10/18	353/17	\times Aseel	19	4	2	9	5
39	17/18	98/16	\times 44/16	44 ²	1	3	4	11
40	20/18	95/15	\times 271/16	31	9	5	17	11
41	22/18	150/17	\times 119/17	(δ)	2	2	6	—
42	10/19	322/17	\times R. I. B.	(δ)	4	2	12	7
45	- 21/18, - 11/19	320/17	\times { 114/17 Buttercup	(δ)	1	4	6	6
					108	93	248	222
From A above					126	136		
Totals					234	229		

¹ See p. 39.² See p. 40.

(a) Grandson from Exp. 43 (cf. p. 39).

(b) Granddaughter of F_1 hen

(c) Granddaughter from Exp. 43 (cf. p. 39).

(d) Granddaughter from Exp. 44 (cf. p. 40).

TABLE II.

A. From henry ♂.						B. From henry ♀.				
	No. of Exp.	Males	Females	Normal Males	Henry Males	No. of Exp.	Males	Females	Normal Males	Henry Males
Families with excess of ♀ ♀	1	33	52	14	8	28	7	12	4	1
	10	19	31	8	11	30	2	4	1	1
	15	4	10	—	4	37	11	16	4	7
	16	10	26	4	6	39	4	11	1	3
	22	5	9	1	3	—	—	—	—	—
Totals	...	71	128	27	32		24	43	10	12
Families with excess of ♂ ♂	6	16	8	5	7	24	24	12	11	8
	17	7	3	3	4	25	15	10	6	3
	19	5	1	3	1	32	20	13	14	5
	20	20	11	9	10	38	9	5	4	2
	—	—	—	—	—	40	17	11	9	5
	—	—	—	—	—	41	6	—	2	2
	—	—	—	—	—	42	12	7	4	2
Totals	...	48	23	20	22		103	58	50	27
Families with proportions of sexes nearly equal	2	21	15	10	10	23	29	36	10	15
	3	13	11	7	6	26	14	14	6	8
	4	5	4	2	3	27	13	11	2	1
	5	39	33	9	17	29	11	12	6	5
	7	12	11	5	6	31	11	12	5	5
	8	19	22	8	9	33	9	7	3	4
	9	21	28	12	8	34	8	7	3	5
	11	9	9	3	4	35	9	7	7	2
	12	23	22	7	8	36	11	9	5	5
	13	12	9	7	2	37	11	16	4	7
	14	13	11	3	5	45	6	6	1	4
	18	10	10	4	4	—	—	—	—	—
	21	8	9	2	—	—	—	—	—	—
Totals	...	205	194	79	82		132	137	52	61

EXPLANATION OF PLATES.

PLATE VII.

Fig. 1. Saddle feathers from an intermediate cock with a marked tendency to normal plumage. The feathers were gold throughout, and were removed when the bird was 28 weeks old.

Fig. 2. Saddle feathers from brother of above bird taken after the moult. Before the moult the feathers of this bird were of the type shewn in Fig. 1. (Cf. p. 42.)

Fig. 3. Feathers from saddle of slightly intermediate bird taken before the moult. The fringes of the two "tipped" feathers are gold in colour.

Fig. 4. Two henry feathers from saddle of above bird taken after the moult. All of the feathers were of this type.

PLATE VIII.

Fig. 1. Saddle feathers of an intermediate with a marked tendency to normal plumage. Feathers taken before the moult.

Fig. 2. Henny saddle feathers of an intermediate taken after the moult. Before the moult the feathers were similar to those shewn in Fig. 1.

Fig. 3. Saddle feathers of same bird taken after the fourth moult. They are of intermediate type and fringed with gold.

Fig. 4. Henny saddle feathers of same bird taken after the fifth moult. (Cf. p. 42.)

PLATE IX.

Skins of two cocks bred from Silver Hamburg ♀ × Gold Hamburg ♂ (Exp. 30). On the left (1) a henny and on the right (2) a normal feathered bird. Both were kept over the moult before being killed.

PLATE X.

Skins of two intermediate feathered birds, from same mating. No. 1 was killed at 9 months while No. 2 was killed a year later. Before the moult No. 2 closely resembled No. 1 in the nature of its feathering. (Cf. p. 42.)

PLATE XI.

1. Skin of henny ♂. General colour warm brown.
2. Skin of castrated henny ♂ 204/15, in general colour closely resembling a Brown Leghorn. Before castration he resembled No. 1. (Cf. p. 49.)

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Fig. 1. ♂ 105/18 (12. 11. 18)



Fig. 2. ♂ 104/18 (1. 8. 20)



Fig. 3. ♂ 104/15 (24. 4. 16)



Fig. 4. ♂ 104 15 (21. 10. 16)



Fig. 1. ♂ 126/15 (14. 11. 15)

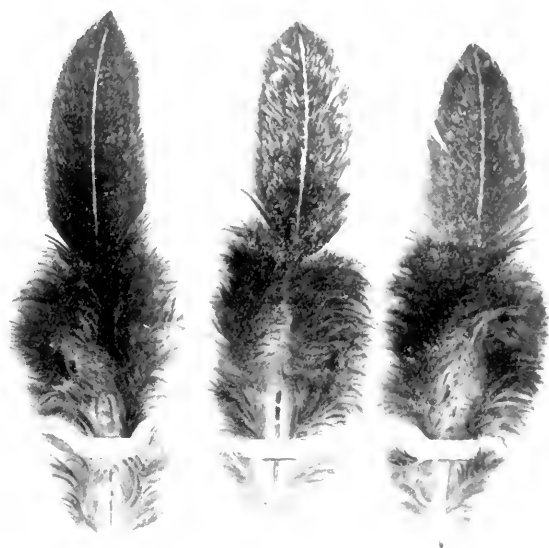


Fig. 2. ♂ 201/14 (8. 11. 15)



Fig. 3. ♂ 201/14 (19. 9. 18)



Fig. 4. ♂ 201/14 (8. 4. 20)





1



2



1



2

A MENDELIAN EXPERIMENT WITH ABERDEEN- ANGUS AND WEST HIGHLAND CATTLE.

By J. A. S. WATSON, B.Sc., M.C.

(With Plate XII.)

WHILE Mendelian analysis has been very successfully applied to the study of the heredity of the smaller animals and of plants, very little progress has so far been made in the investigation of the mode of inheritance of the characters of the larger and more important domesticated animals. This fact is of course sufficiently explained by the obvious difficulties—the large financial outlay and the extended period of time necessary to obtain experimental results. It would appear, however, that there is no alternative to the method of tedious breeding experiments if the many and important problems connected with animal breeding are to be solved. A certain amount of progress has indeed been made by the study of records contained in herd- and stud-books, but it is certain that the results of such investigations lack the scientific conclusiveness of those of carefully planned and critical experiments. Thus such an apparently simple question as that of the inheritance of the red, white and roan colours in Shorthorn cattle, on which practically unlimited statistical evidence is available, has been investigated by several workers, and three quite distinct Mendelian interpretations have been proposed—by Wilson (1), Laughlin (2), and Wentworth (3), respectively—no one of which gives a complete and satisfactory explanation of the facts.

The present experiment was commenced in 1910; the object laid down was to determine the mode of inheritance, in crosses between Aberdeen-Angus and West Highland Cattle, of the horned and polled conditions, of colour differences, of hair characters and of differences in conformation. The two breeds may be briefly described. The Aberdeen-Angus is black in colour, with the exception that a small amount of white is permissible on the underline behind the umbilicus, and on the end of the tail. It is hornless, with a relatively short, smooth coat, and is of the early-maturing beef type—i.e. short of leg, blocky, wide, heavily fleshed and small boned. With regard to the purity, in the Mendelian

sense of the colour and of the hornless condition, it is to be noted that red calves are occasionally born from pure bred black parents even in the most carefully selected herds. White markings, beyond those permitted by the breed standard also occur at times, more particularly white feet. Horns, or more generally what are called "scurs"—small, firm or loose horny excrescences—were once comparatively common but have now been all but eliminated by selection.

The general character of West Highland cattle is well known. They carry large spreading horns, a long and shaggy coat, and are of beef type, short of leg and blocky but distinctly narrower in build and less heavily fleshed than the Aberdeen-Angus. They are also characteristically later in reaching maturity and less readily fattened. The colours are many—red, black, yellow, dun and brindled—accurate classification being somewhat difficult in a percentage of cases. In the present experiment cattle of only two colours were included—viz. red and dun.

Four different pedigreed Angus bulls were employed in the experiment, and were mated to seven different pure bred West Highland cows. Apart from the latter, two cows, which happened to be available, were included, the result of a cross between the Chartley (a white horned breed, with black "points") and the West Highland. One female of the Angus \times Chartley-Highland cross was retained for breeding. The inheritance of the individual characters may now be considered.

(1) COAT AND CONFORMATION.

Unfortunately no data worth presenting were obtained with regard to the inheritance of these characters. Attempts were made during the earlier part of the experiment to reduce the descriptions of the coat to actual measurements of the length and diameter of the hairs. The main difficulty, apart from that of sampling, was that the seasonal differences varied greatly as between different animals—e.g. an animal which had a relatively heavy winter coat might have a relatively light summer coat. Again the hair development is influenced by causes other than heredity, notably by the "condition" or degree of fatness, and pregnancy. The value of these measurements was therefore doubtful, but frequent and regular examination might still have yielded something of interest. The author, however, was able to see the cattle only at rare and irregular intervals during the period of the war, and this line of investigation was of necessity given up. The general impression made by the cattle was that the first hybrid generation was intermediate with regard to coat.

The individuals were similar in coat character, with one exception (♀ No. 8), which was distinctly shorter haired. In F_2 there was certainly some form of segregation, individuals being obtained which approached somewhat the Highland type and others which were almost or perhaps quite as smooth as the average Angus (cf. Pl. XII, fig. 2). The distribution, however, suggested a ratio considerably more complex than the simple monohybrid one of 1 Rough:2 Intermediate:1 Smooth. With regard to conformation, certain of the F_2 suggested rather strongly, in one or other point, one of the parental types; but no statement beyond this would be justifiable.

(2) HORNS AND COLOUR.

Below follows a descriptive list of all the animals bred during the course of the experiment.

(a) *Horns.*

The existing true breeding types of cattle are either (a) horned in both sexes, or (b) polled in both. The third possible condition, which is found for example in certain breeds of sheep, in which the males bear horns while the females are hornless, is not known among living cattle, though Major (4) has described this condition in skulls from the tertiary deposits in Italy.

F_1 Generation.

Ref. No.	Sex	SIRE		DAM		Date born	Horns	Colour	Remarks
		Ref. No.	Breed and description	Ref. No.	Breed and Description				
F_1 1	♂	AA 1	Angus-Black-Polled	H 1	W. Highland Dark Red, Horned	Dec. 1911	Short horns	Black	
F_1 2	♀	AA 3	„	H, C 3	Highland × Chartley Reddish Dun, Horned	Feb. 1912	Polled	Dun	
F_1 3	♂	AA 3	„	H, C 4	Highland × Chartley Reddish Dun, Horned	Apr. 1912	Polled	Red	Sold at 3 months old
F_1 4	♂	AA 1	„	H 2	Highland Dark Red, Horned	May, 1912	?	Black?	Still born
F_1 5	♀	AA 2	„	H 5	Highland Yellow Dun, Horned	Jan. 1912	Polled	Dun	
F_1 6	♀	AA 2	„	H 6	Red Horned	Dec. 1911	Polled	Black	
F_1 7	♀	AA 2	„	H 7	Red Horned	Jan. 1912	Polled	Black	
F_1 8	♀	AA 4	„	H 9	?* Horned	June, 1911?	Polled	Black	
F_1 9	♀	AA 4	„	H 9	?* Horned	Feb. 1912?	Polled	Black	

* F_1 No. 8 and No. 9 were purchased as yearlings. Their descent from a pedigreed Angus bull and pure bred Highland cows was unquestionable, but their particular dams could not be identified with certainty. The latter were probably red.

F₂ Generation.

Ref. No.	Sire	Dam	Calved	Sex	Horns	Colour
<i>F</i> ₂ 1	<i>F</i> ₁ 1	<i>F</i> ₁ 2	1914	Female	Polled	Black
<i>F</i> ₂ 6	"	"	1915	Female	Horned	Dun
<i>F</i> ₂ 11	"	"	1916	Female	Polled	Dun
<i>F</i> ₂ 17	"	"	1917	Female	Polled	Silver Dun
<i>F</i> ₂ 23	"	"	1918	Female	Polled	Red
<i>F</i> ₂ 2	<i>F</i> ₁ 1	<i>F</i> ₁ 5	1914	Female	Polled	Black
<i>F</i> ₂ 7	"	"	1915	Female	Polled	Dun
<i>F</i> ₂ 12	"	"	1916	Male (cast.)	Polled	Red
<i>F</i> ₂ 18	"	"	1917	Female	Polled	Dun
<i>F</i> ₂ 3	<i>F</i> ₁ 1	<i>F</i> ₁ 6	1914	Female	Polled	Black
<i>F</i> ₂ 13	"	"	1916	Male (cast.)	Horned	Black
<i>F</i> ₂ 19	"	"	1917	Female	Horned	Red
<i>F</i> ₂ 24	"	"	1918	Female	Polled	Red
<i>F</i> ₂ 4	<i>F</i> ₁ 1	<i>F</i> ₁ 7	1914	Male (cast.)	Hardscurs under hair	Black
<i>F</i> ₂ 8	"	"	1915	Male (cast.)	Horned	Black
<i>F</i> ₂ 14	"	"	1916	Female	Horned	Black
<i>F</i> ₂ 20	"	"	1917	Female	Polled	Red
<i>F</i> ₂ 25	"	"	1918	Female	Polled	Black
<i>F</i> ₂ 5	<i>F</i> ₁ 1	<i>F</i> ₁ 8	1914	Female	Polled	Black
<i>F</i> ₂ 9	"	"	1915	Male (cast.)	Horned	Black
<i>F</i> ₂ 15	"	"	1916	Male (cast.)	Horned	Black
<i>F</i> ₂ 21	"	"	1917	Female	Polled	Black
<i>F</i> ₂ 22	"	"	1918	Male	Polled	Black
<i>F</i> ₂ 10	<i>F</i> ₁ 1	<i>F</i> ₁ 9	1915	Female	Polled	Black
<i>F</i> ₂ 16	"	"	1916	Female	Polled	Black

Note. There is some doubt about the respective dams of *F*₂ 13 and 14 and 19 and 20. It is possible that the dams are reversed in either case or both, i.e. 13 and 19 may be from *F*₁ 7 and 14 and 20 from *F*₁ 6.

In the present experiment the *F*₁ generation females were all "clean polled," i.e. without any trace of horn development. *F*₁ No. 3, a bull calf, was sold for slaughter at three months of age, at which time no horn development had occurred. The bull *F*₁ No. 1 (Pl. XII, fig. 1) developed peculiar short stout horns, which grew at an abnormally slow rate. At 18 months they were about 4 ins. long. At 6 years they measured 10 ins. There can be no doubt that this animal, like the other *F*₁ crosses, was heterozygous for the polled character. We should therefore conclude that the polled condition is completely dominant in the female, while in the hybrid male the horn development is inhibited, but at least not always completely suppressed. These results are in accord with those of Gowen (5) who obtained the following in first hybrids between Aberdeen-Angus and various horned breeds.

Horned		Hard scurs		Loose scurs		Polled	
Male	Female	Male	Female	Male	Female	Male	Female
2	0	3	0	7	1	2	10

On the other hand, Lloyd Jones and Evvard (6), in crossing the Galloway (polled) and Shorthorn obtained the following in 78 F_1 :

70 Clean Polled,
6 Seurred,
2 Horned.

Unfortunately the sexes of the eight exceptional animals are not given, but the two horned animals are attributed by the authors, with much reasonableness, to the probably impure condition (with regard to hornlessness) of certain "grade" Galloway cows which were included in the experiment; and they found "no evidence that sex is in any way connected with the inheritance of these characters." Against this it may be mentioned that among crosses between Red Polls and Ayrshires at present being bred in Dumfriesshire, a large proportion of the F_1 males bear horns. It appears certain that the degree of dominance of the polled character in the male varies according to the particular breeds employed, and varies too as between different individuals of the same cross.

In the present experiment the distribution of horns in F_2 was as follows:

			Polled	Hard "seurs"	Normal horns
Females	15	—	3
Males (castrated)	2	1	4
Totals	17	1	7

Including the male with "seurs" as polled, we obtain the numbers 18 polled, 7 horned, which agrees very closely with the simple Mendelian ratio of $3D:1R$. As the numbers are small, it is probably worth while to combine them with those obtained by Lloyd-Jones and Evvard in the F_2 of the Galloway \times Shorthorn cross above referred to, thus:

		Female		Male		Totals	
		Polled	Horned	Polled	Horned	Polled	Horned
Present Experiment	...	15	3	3	4	18	7
Lloyd Jones and Evvard...	...	9	4	7	1	16	5
Totals	...	24	7	10	5	34	12
Expectation ($3D:1R$)		23.25	7.75	11.25	3.75	34.5	11.5

The numbers are again in very close agreement with the hypothesis, originally advanced by Bateson and Saunders (7) and Spillman (8 and 8a), that the horned and polled conditions form a simple pair of Mendelian characters.

To revert to the question of dominance in the male, Wood (9) and Arkell (10) have found that in crosses between horned and hornless

breeds of sheep, the heterozygous males are horned, while the heterozygous females are hornless. The horn development in the hybrid male has been shown to be dependent on a hormone secreted by the testis, and horn growth is stopped (again in the hybrid) by castration. The analogous experiment has not been performed with cattle. It is to be noted that the F_2 males were all castrated.

(b) *Colour.*

The F_1 generation, with the sole exception of the red calf F_1 3, were either dun or black. With regard firstly to the behaviour of black and red, we should conclude that black is dominant, red recessive. Matings of the heterozygous F_1 blacks *inter se* (F_1 females 6, 7, 8 and 9) produced 16 F_2 of which 13 were black, 3 red, against an expectation of 12 and 4. These results may be regarded as in complete accord with the accepted view, originally advanced by Spillman (11) that red behaves as a simple recessive to black. The red calf F_1 3 calls for further explanation, but a highly probable explanation is at hand, namely that its Aberdeen-Angus sire AA 3 was heterozygous for black. The appearance of the recessive reds in pure bred Angus herds, already referred to, renders such an explanation inherently probable. Moreover the bull in question was in use by a local farmer for crossing with heifers of mixed colours, and with them he begot a large proportion of red and red-roan calves. In this connection it may be said that the sires AA 2 and AA 4 left no red calves in the herds where they were used on cattle of various colours. AA 1 cannot be regarded as having been tested.

The dun \times black matings constitute a more complex problem. The hypothesis thus far proposed must first be considered. Wilson (12 and 13) has proposed a series of Multiple allelomorphs or "polygamous factors," any one of which behaves as a Mendelian alternative to any other. In so far as the present experiment is concerned, three factors would be concerned, viz. B (black), R (red), and L (Light Dun). The following are the colours allotted by Wilson to the various possible factor combinations:

BB	Black (homozygous)
BR	Black (heterozygous)
BL	Dun
RR	Red
RL	Yellow
LL	Light Dun

According to this the dun F_1 females 2 and 5 would be BL and the F_1 male of course BR . The chances of the various combinations would be

$I BB$	Black (homozygous)
$I BR$	Black (heterozygous)
$I BL$	Dun
$I RL$	Yellow

We should therefore expect a ratio of

2 Black : 1 Dun : 1 Yellow.

The obtained results :

2 Black : 5 Dun : 2 Red,

not only suggest a different ratio, but give a colour which is not provided for by the scheme. As has already been pointed out by Babcock and Clausen (14), Lloyd Jones and Evvard in the experiment, already alluded to, obtained 6 reds out of 26 F_2 in crosses of White Shorthorn and Galloway, which again are inexplicable on Wilson's theory. The latter, in its present form, must therefore be regarded as inadequate.

Wright (15), on the contrary, has proposed a system of ordinary unit factors, only two of which would be concerned in the present case, viz. :

E , black, its absence e giving red, and

D , a dominant pigment dilution factor, in whose presence black is modified to dun, and red to yellow. The nine possible factor combinations give the following respective colours :

$ddEE$	Black, homozygous
$ddEe$	Black, heterozygous
$ddee$	Red
$DdEE$	Dun (homozygous for black factor)
$DdEe$	Dun (heterozygous for black factor)
$Ddee$	Yellow
$DDEE$	Cream dun (homozygous for black factor)
$DDee$	Cream (light dun)

On this hypothesis the male F_1 1 would be $ddEe$, and both dun females, F_1 2 and F_1 5, $DdEe$ ¹. The possible combinations and the probable frequency would then be :

¹ No. 5 might conceivably have been $DdEE$, although the chances are slight, black being a comparatively rare colour among Highland cattle. The fact that she produced a red calf, however, shows definitely that she was heterozygous for the black factor.

1 <i>DdEE</i> (dun), 2 <i>DdEe</i> (dun)	= 3 dun
1 <i>Ddee</i> (yellow)	= 1 yellow
1 <i>ddEE</i> (black), 2 <i>ddEe</i> (black)	= 3 black
1 <i>ddee</i> (red)	= 1 red.

The results obtained, 5 dun, 2 black, 2 red, while not agreeing closely with expectation, contain nothing that is definitely opposed to Wright's hypothesis.

It is obvious, however, that, so far as concerns the present experiment, a third explanation is possible, which has the merit of greater simplicity, viz. that the factor *D* is not a colour dilution factor, modifying both black and red, but an independent factor for dun colour, epistatic to *E* (black), and producing dun whenever present. This hypothesis would give an expected ratio of 4 dun, 3 black, 1 red, which is comparatively near to the ratio obtained. The numbers are, however, obviously too small to furnish any definite proof of such an hypothesis.

CONCLUSIONS.

(1) The polled and horned conditions form a simple Mendelian pair. The polled condition is completely dominant in the female, while in the heterozygous male horn development is inhibited but not always suppressed.

(2) Black is dominant to red, and the colours behave as a simple Mendelian pair.

(3) The hypothesis of multiple allelomorphs for colour, proposed by Wilson, is not in agreement with the results obtained.

(4) Dun is dominant to black, but whether as a simple epistatic, or whether produced by a dilution factor capable of modifying colours other than black, does not appear from this experiment.

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Fig. 1. F_1 Bull at 2 years 9 months old.

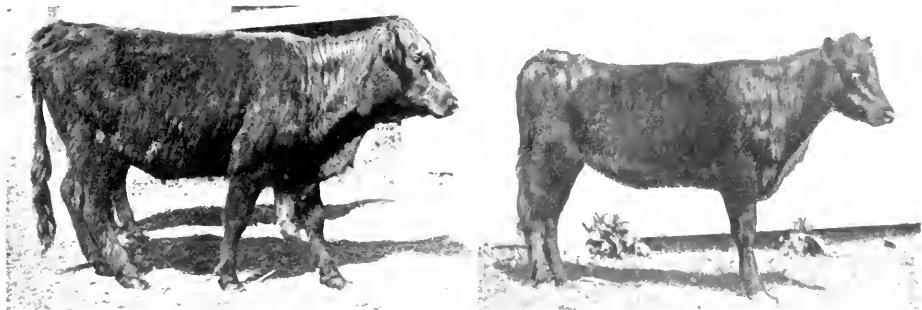


Fig. 2. F_2 Yearling heifers showing extreme types of coat. Of similar age, and from the same lot.



Fig. 3. Dun F_1 Cow with Black F_2 Calf.



EXPLANATION OF PLATE XII.

Fig. 1. F_1 ♂ (No. 1) at 2 years 9 months old.

Fig. 2. Two F_2 yearling heifers shewing extreme types of coat.

Fig. 3. Dun F_1 cow with black F_2 calf.

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NOTE ON THE EVOLUTION OF THE DOUBLE STOCK (*MATTHIOLA INCANA*).

BY EDITH R. SAUNDERS,
Fellow of Newnham College, Cambridge.

(With Three text-figures.)

THE question whether the fully double Stock, as we know it to-day, arose in the first instance by a single considerable mutation producing the form with which every flower lover is familiar, must have arisen in the minds of many horticulturists since the plant became a favourite in our gardens. So far as I am aware no statement exists as to when, where or by whom the double form was first observed. The earliest reference known to me, as I have stated elsewhere¹, is that by Dodoens² in 1568. In this account as in the later illustration by de l'Obel and Pena³ (1576) it is a full double which is depicted, a double, that is, destitute of any semblance of either stamens or carpels. In view of this testimony and of the further facts (1) that all double Stock strains now in cultivation are of this fully double type, (2) that we know that in the case of certain other genera having different grades of doubles (Wallflower, Lobelia) the appearance of the full double *preceded*—in the former case probably by some centuries—that of the semi-double, (3) that in a full double of such recent origin as *Arabis albida* we have no knowledge of any intermediate stage in the doubling process, we may safely accept the evidence for the mutation having been accomplished in the Stock by a single step as amounting to proof. Nevertheless we meet with some records in the literature dealing with *Matthiola* which might be construed as conflicting with this view, and which in any case call for some further explanation. I have been unable until now to come to any definite conclusion in regard to this counter-evidence, but certain specimens noticed of late in my own cultures appear to me to provide the solution. I have therefore thought

¹ "The Double Stock, its History and Behaviour," *Journal Roy. Hort. Soc.* Vol. XI, Part III. 1915.

² *Florum et coronariarum*.....

³ *Stirpium adversaria nova*.

it worth while to put these observations on record and so clear the ground of any doubt which these earlier references, as they stand, might throw on the validity of the conclusion expressed above. Taking the references in question in their chronological order we have:

(1) Sowerby's illustration of *Cheiranthus incanus* in the first and second editions of *English Botany*¹. The specimen figured was obtained in 1808 by lowering a boy over the cliffs near Hastings. It is on record that Hooker was present on the occasion as well as Borrer (who with Dawson Turner discovered the plant in this locality in 1806), and it may be inferred from the account that only the one specimen was taken. The illustration represents a simple raceme on which only four flowers are as yet open, the remainder being still in the bud stage. The first (lowest) of these is shown viewed from the back with only calyx and corolla visible. Both appear to be normal. In the succeeding (second) flower there are nine petals of about normal size and an additional very small one in the centre where only three out of the four long stamens appear. The third flower is shown with five petals and the anthers of the four long stamens. In the fourth flower we have, so far as can be judged, again a normal single. Now it is to be noted that in the third edition this illustration is replaced by a drawing of a plant obtained from the Isle of Wight. [The plant had been lost apparently from the Hastings locality as far back as 1835².] I have been unable to trace in botanical writings any allusion to the reason for this substitution and although many of Borrer's specimens are preserved at Kew, I cannot find that the 1808 Stock is among them. It may be presumed, I think, that it is not now in existence. The probable explanation of why it was discarded will appear presently.

(2) A statement in Hopkirk's *Flora Anomala*³ (1817), a work brought to my notice by Dr Agnes Arber. The passage runs as follows: "Of multiply polypetalous flowers we have many examples, as *Cistus helianthemum*, *Anemone nemorosa*, *Sanguinaria Canadensis*, *Tormentilla officinalis*, *Hibiscus mutabilis*, *Tulipa sylvestris*, *Cheiranthus Cheiri*, *Hesperis matronalis*, *Matthiola incana*, and many others. In these instances, the stamens and pistil not being injured, the seeds may be produced as in single flowers." [Multiply is here used to indicate flowers in which the number of petals is augmented without affecting the other parts.]

¹ Vol. xxvii. pl. 1935 in order of issue (Vol. xi. pl. 993 in copies bound in order of systematic relationship).

² See Watson, *The New Botanist's Guide*, p. 51.

³ P. 114.

In a footnote Hopkirk adds the remark—"The semi-double variety of *Hibiscus mutabilis*, frequently produces seeds, and these almost always, in their turn, produce semi-double and double flowers, which the seed from single flowers seldom do, and the same thing may be observed in Stocks, Wallflowers, etc." A pronouncement in such general terms as that contained in the concluding sentence of the footnote we may, I think, without hesitation, disregard. It carries with it a suggestion of being merely the usual repetition of untested tradition, not a confirmation from first-hand observation. I doubt whether Hopkirk's earlier statement is likely to be based on any better authority. Even if well-founded it imports no more, probably, than that other observers have met with the same type of abnormality as that which has occurred in my cultures (see later), the appearance of which has made it possible to clear up the position.

(3) The statement in De Candolle's description of *Matthiola annua* (*Syst.* II. p. 165, 1821) that the flowers are in colour similar to those of *M. incana* and always single or rarely semi-double. (The italics are mine.)

(4) The statement by Phillips (*Flora Historica*, Vol. II. p. 29, 1824) that there is frequently a straggling anther to be found in the double blossoms [of the Stock].

(5) The illustration of *Matthiola incana* in *Flowering Plants and Ferns of Great Britain*, by Anne Pratt, which is very similar to Sowerby's drawing. At the time of writing this work Anne Pratt was living at Dover, at no great distance, therefore, from the spot where Sowerby's specimen had been obtained. But, as stated above, *M. incana* was believed to have disappeared from this locality long before this date¹. We gather from Bromfield² that in the Isle of Wight, another well-known station, the plant, as at Hastings, was by no means easy of access. It was known to occur also on the cliffs of Ramsgate and Broadstairs³, and all three localities are cited by Anne Pratt. From a passing remark⁴ one infers that recourse was not had by the authoress to a garden form as a model, and it is therefore a question of some interest whether she procured a new wild specimen for her plate or whether we may take it that her illustration is a free rendering either of Borrer's original plant or of Sowerby's drawing of it. A comparison of the two plates

¹ 1854 probably, but the first edition is undated.

² *Flora Vectensis*, 1856.

³ Cowell, *Floral Guide to East Kent*, 1839.

⁴ *Loc. cit.* Vol. I. p. 135.

leaves no doubt in my mind that the illustrations both of *M. incana* and of *M. sinuata* in Anne Pratt's work are adapted from Sowerby. One has only to note the number and position of the open flowers and of the unopened buds in the two cases to become convinced on this point. So far then as illustration (as opposed to description) of anything approaching a semi-double Stock goes we need only take account of Sowerby's original plate. In this case we have the categorical statement that the drawing was made from the actual specimen obtained with so much difficulty. It represents, as will be clear from the description given above, a type of individual apparently of an intermediate grade between a normal single and a typical double. Nevertheless, from what follows, it will be seen that it must be regarded as a genuine single, and that the partially double flowers result from a morphological modification different from that of ordinary doubling. It is well known that an additional fifth petal may occasionally make its appearance in one or two flowers on a stock plant otherwise single. We find this abnormality mentioned by Hill¹, Phillips², Chaté³ and others. It is of rare occurrence and appears to have no hereditary significance. We cannot tell on which individual we shall find, among the hundreds of normal flowers produced in the course of the season, one or two with C_5 instead of C_4 . We can however predict with some certainty the position in which, *if present*, these flowers will occur. My experience is that when this abnormal condition exists it is to be found in the lowest flowers on the axes, and among those that open first in the season. That is to say the abnormality is associated with the region and the period of greatest vigour. Now it is also among flowers occupying this position that a more pronounced deviation from the normal is occasionally to be met with, and I feel no doubt that it is this more extreme type of monstrosity which chanced to be exhibited in Sowerby's specimen, and which, occurring now and then, as it evidently does, gave rise to statements such as those quoted above. We may safely conclude that it was the realisation that the original specimen was an aberrant form which led to the substitution of a new plate of *M. incana* in the third edition of *English Botany*. The modification in this case arises from a more or less complete "twinning" of a normal single flower. Figs. 1 and 2 represent two instances of imperfect twinning occurring, in each case, in the first (lowest) flower of the inflorescence.

¹ *Eden*, p. 567, 1757.

² *Loc. cit.*

³ *Cult. prat. des Giroflées*, pp. 63, 64.

In plant *A* (Fig. 1) the "flower" showed 5 sepals, 6 petals, 10 stamens (only those extending above the stigmas are shown) and a gynoeceium with 4 distinct stigma lobes terminating what appeared to be 4 carpels

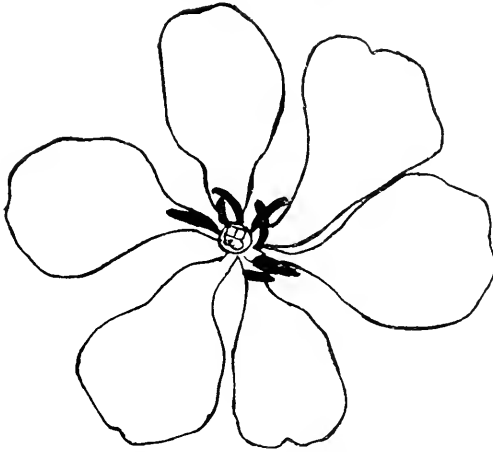


Fig. 1. The lowest "flower" on the main axis of plant *A* viewed from above, showing imperfect "twinning" (slightly enlarged).

showing slight torsion and incomplete fusion along one suture so that the ovules were exposed. In plant *B* (Fig. 2) the calyx was formed of 6 sepals arranged in two groups of three. As in the previous case there were 6 petals and 10 stamens of which eight only are here represented,

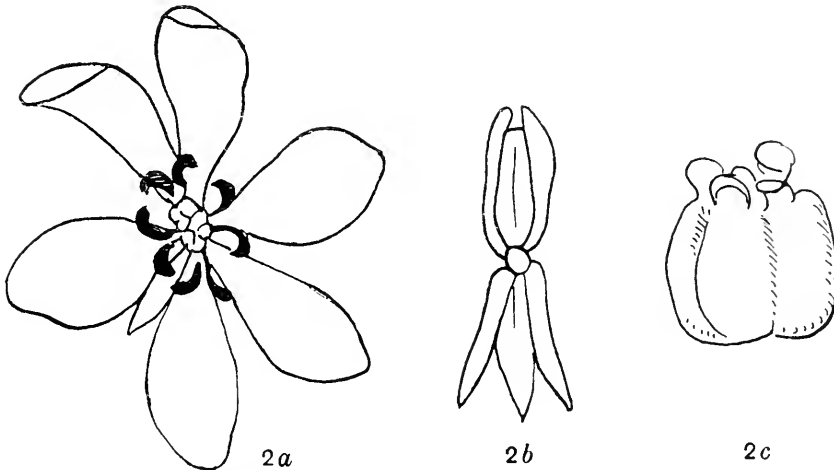


Fig. 2. A similar case from another plant *B*. *a* "flower" viewed as in Fig. 1, *b* calyx seen from below, *c* monstrous gynoeceium (considerably enlarged).

the other two being hidden. The monstrous gynoeceium resulting from the twin ovaries appeared to have 5 stigma lobes. In Fig. 3 taken from a flower in the same position on a lateral axis of a third plant (*C*) the

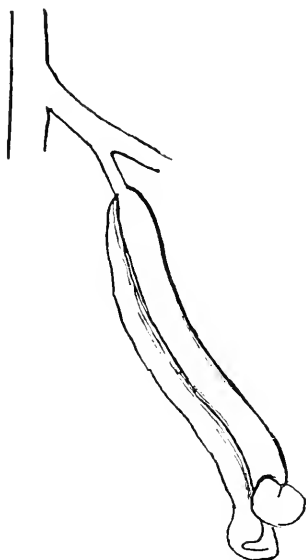


Fig. 3. Nearly mature fruit from the lowest "flower" on the first lateral branch of a third plant *C* (much foreshortened). A distinct furrow occurs on both sides in the dividing plane.

twin nature of the gynoeceium is seen at a very much later stage. In the case of plant *A*, the only one examined for this point, the pedicel was somewhat thicker than usual and showed, on cross section, an elliptical instead of the normal ring arrangement of the fibro-vascular bundles, characteristic of the true double as well as the single. The stouter form of the pedicel can be detected in Sowerby's drawing (second flower) and though slight, the increase is no doubt faithfully portrayed. The fact that the twin flowers appear to develop from a common basis accounts for the incomplete duplication of the parts on the adaxial sides. We get no indication from Sowerby's figure (owing to the view presented) of the composition of the calyx and gynoeceium of the second flower, but if my interpretation is correct we have here a case of twinning carried to a further stage, combined, apparently, with petalody of at least one member of the androeceium. We may include in the same category no doubt the case observed by Master's¹ and described under the head of synanth². Here duplication of calyx, corolla and androeceium was all but complete, only the two short stamens at the point where separation was imperfect being suppressed. We may then I think conclude, notwithstanding the statements of various writers which might be interpreted to the contrary, that there is no case on record of a genuine semi-double Stock; and that the records in question owe their origin to the occasional occurrence of more or less perfect "twinning" of the lowest flowers on the earliest flowering axes.

I wish, in conclusion, to express my grateful thanks to Miss D. F. M. Pertz who kindly made the drawings from my plants.

¹ *Vegetable Teratology*, p. 38, 1869.

² I have intentionally refrained from using this term in the present instance in order to avoid the implication that in the normal condition there are two distinct flowers which become occasionally more or less fused together.

THE ANALYSIS OF THE RESULTS OF PROFESSOR JOHANNES SCHMIDT'S DIALLEL CROSSINGS WITH TROUT.

By H. L. TRACHTENBERG, B.A. (CANTAB.), A.I.A.

Actuarial Assistant in the Statistical Department of the Medical Research Council.

IN the *Journal of Genetics* for December, 1919, Professor Johannes Schmidt described an experiment on trout¹. The basis of this experiment was his method of diallel crossings in which each female is crossed with each male, and the character measured was the number of vertebrae.

In analysing his results, he sought for a "simple rule connecting the number of vertebrae in the offspring with that in the parents." He first distinguished between "the realized purely *personal* value of a given individual trout—this value would have been a different one if the individual in question were developed in different environments—and the *generative* value of the same individual, and that is the value which it imparts to its offspring." He then assumed that "the average for a number of offspring-individuals closely coincides with the average of the generative values of the parents," and proceeded to inquire whether this supposition did agree with the values arrived at in the experiment. He obtained, however, insufficient independent equations for a solution of the problem, and had recourse to an arbitrary assumption to give him the necessary additional equation. This arbitrary assumption is unnecessary. I will demonstrate this, and indicate my alternative process.

On the basis of his original assumptions Professor Schmidt writes down the twelve equations connecting the offspring averages with the means of the generative values of the parents:

$$\frac{x+a}{2} = 61.14, \quad \frac{y+a}{2} = 61.35, \quad \frac{z+a}{2} = 60.65, \text{ etc.,}$$

¹ "Racial Studies in Fishes. III. Diallel Crossings with Trout (*Salmo Trutta* L.)." By Johs. Schmidt, D.Sc., Director of the Carlsberg Physiological Laboratory, Copenhagen. *Journal of Genetics*, Vol. ix. No. 1, pp. 61—67.

where x, y, z, a, b, c, d are now understood to refer to the generative values of the parents. These are written in the form of equations but he indicates of course that exact equality is not expected, differences between the two sides being allowed in the degree permitted by the variation of the measurements in the samples. He therefore combines them into seven equations, which are in fact the seven equations yielded by applying the method of least squares. Unfortunately these seven equations are not independent. They are equivalent to but six independent equations and thus could be satisfied in an indefinite number of ways. To obtain another equation Professor Schmidt assumed that the generative value of one of the parents (y) coincided with its personal value (60). This is the arbitrary assumption referred to above. I surmount the difficulty as follows. Seven equations which are all independent and therefore do not require recourse to any arbitrary assumption can be obtained if in writing down the original relationships, account be taken not only of the relation of the offspring average measurements to the average parental generative values, but of the parental individual measurements to the parental generative values. In other words we have simply to set out to find such values of x, y, z, a, b, c, d as will satisfy the twelve offspring equations

$$\frac{x+a}{2} = 61.14, \quad \frac{y+a}{2} = 61.35, \text{ etc.}$$

and the seven parental equations

$$x = 59, \quad y = 60, \text{ etc.,}$$

such differences being allowed as are permitted by the degree of variation of the measurements. Since the sample is 50 in the case of the offspring-averages, and but unity in the case of the parent measurements, a greater divergence is permitted between the two sides of the parent equations.

The equations duly weighted by $\sqrt{50}$, prepared for the application of the method of least squares are :

x	=	59
y	=	60
z	=	59
a	=	61
b	=	59
c	=	57
d	=	58

$$\sqrt{50} \frac{x+a}{2} = \sqrt{50} \ 61.14$$

$$\sqrt{50} \frac{x+b}{2} = \sqrt{50} \ 59.06$$

$$\sqrt{50} \frac{x+c}{2} = \sqrt{50} \ 58.29$$

$$\sqrt{50} \frac{x+d}{2} = \sqrt{50} \ 59.03$$

$$\sqrt{50} \frac{y+a}{2} = \sqrt{50} \ 61.35$$

$$\sqrt{50} \frac{y+b}{2} = \sqrt{50} \ 59.22$$

$$\sqrt{50} \frac{y+c}{2} = \sqrt{50} \ 58.59$$

$$\sqrt{50} \frac{y+d}{2} = \sqrt{50} \ 59.28$$

$$\sqrt{50} \frac{z+a}{2} = \sqrt{50} \ 60.65$$

$$\sqrt{50} \frac{z+b}{2} = \sqrt{50} \ 58.48$$

$$\sqrt{50} \frac{z+c}{2} = \sqrt{50} \ 57.90$$

$$\sqrt{50} \frac{z+d}{2} = \sqrt{50} \ 58.55.$$

The seven equations for solution yielded by these are :

$$51x + 12.5(a+b+c+d) = 5997$$

$$51y + 12.5(a+b+c+d) = 6021$$

$$51z + 12.5(a+b+c+d) = 5948.5$$

$$38.5a + 12.5(x+y+z) = 4639.5$$

$$38.5b + 12.5(x+y+z) = 4478$$

$$38.5c + 12.5(x+y+z) = 4426.5$$

$$38.5d + 12.5(x+y+z) = 4479.5.$$

These are all independent and supply definite values of

$$x, y, z, a, b, c, d.$$

The following Table shows the theoretical figures against the actual.

Parents		Offspring	
Personal Value	Generative Value	Mean of personal values of group of 50	Mean of Generative values of Parents
59	59.78	61.14	61.11
60	60.25	59.06	59.01
59	58.83	58.29	58.34
61	62.44	59.03	59.03
59	58.24	61.35	61.34
57	56.90	59.22	59.25
58	58.28	58.59	58.58
—	—	59.28	59.27
—	—	60.65	60.63
—	—	58.48	58.54
—	—	57.90	57.87
—	—	58.55	58.55

It will be noticed that like Professor Schmidt's results the average values for the offspring are much closer to the means of the generative values of the parents, than are the personal values of the parents to their generative values. The most extreme individual difference is 61 personal value against 62.44 generative value. Though this is less marked than Professor Schmidt's contrast between a personal value of 61 and a generative value of 62.72, it is still capable of bearing his conclusion as to the marked difference that can occur between the personal value and the generative value of an individual.

NOTES ON BREEDING FOR INCREASE OF MILK IN DAIRY CATTLE.

By ELIZABETH ROBERTSON.

(With Eight Pedigree Charts.)

THE following paper deals with the breeding of Dairy Cattle. The subject is one of great complexity, and the methods suggested are, I am aware, open to statistical criticism. Much more work is required before the principles urged can be considered as fully established, but the results are sufficiently striking to justify this statement in the hope that other breeders may be induced to try to improve their stock along similar lines. The breed used is the Kerry, one of the remnants of the Celtic cattle that are supposed in pre-Roman times to have covered the Continent of Europe and to have been gradually replaced by breeds from elsewhere brought by the Romans. They are longer and narrower in the skull and face as well as smaller than the Long Horns, Shorthorns and Herefords. For size they stand midway between the Jersey and the Ayrshire and obviously have far more affinities with the former than with the latter. When used for cross breeding they are strongly prepotent. Being comparatively few in numbers they are apt to be inbred, and being for the most part in uneducated hands the inbreeding has been casual.

The contents of the paper may be briefly summarized as follows :

1. Inbreeding to a male relationship tends to increase both the quantity and the quality of the milk produced.

2. Inbreeding to a female relationship tends to decrease both the quantity and the quality of the milk produced, especially the quantity.

In Table I, the three tables of male inbreeding include 26 cases of which five were failures in respect of quantity. One of these cows (No. 109) failed to retain the milk in the udder ("ran out") but not taking this into account she is included as though she had been a normal cow. The results are (discarding the decimals) 80 % of cases in which the cows showed an increase of milk when compared with the record of

the dam and 20% which showed a decrease in the yield of the cow when compared with her dam.

In Table II are given the results : (a) of mixed inbreeding to both male and female relationships, the male being the nearer and therefore, presumably, the stronger. It will be noted that though there are only 10 cases the percentages showing increase of milk and decrease of milk are respectively 80% and 20%, (b) mixed inbreeding with the female relationship the nearer, these are all decreases.

Table III gives out- or chance-breeding experiments and its results. There are 31 cases of these—only four were increases, i.e. 87% showed a decrease in milk yield and 13% an increase.

The pedigrees attached explain what is meant by related breeding. It may be described as "the mating of a bull with a cow who is so related to him that their first common ancestor is a bull" or in other words, one or more bulls must be repeated in both the sire and dam's pedigrees. These, then, become "links," i.e. linking bull or bulls and make a malely related breeding.

A femalely related breeding is described in the same terms substituting cow for bull.

Full relationships are made when the same bull and cow give rise to the animals "through" whom the link is carried on. It is interesting to note that breeding to full relationships appears to produce a maintenance of the dam's record in her female calves.

In Pedigree IV Gort Sheen ♂ is mated to Mona ♀ in both pedigree of sire and dam and the full brother and sister Vaddy Sheen ♂ and Glenelly ♀ ultimately make a "full" first cousin once removed relation between their descendants Burntollet II ♂ and Glenelly II ♀.

Pedigree V illustrates a "nearly full" relationship.

H, *B*, and *S* is an abbreviation for half brother and sister.

Avunc. is an abbreviation for Avuncular relationship, i.e. Uncle and niece or Aunt and nephew.

1st once signifies first cousin once removed and so on.

The third lactation is taken as the standard year and most cows do reach their full development then.

In Table IV sundry tables are given :

(1) The annual average of butterfat for the whole herd showing the gradual rise as the herd became more and more "bred."

(2) A table showing the results of classifying the heifer by the rise of the yield in milk in comparison with their dams' records in quantity and quality.

The difficulties of breeding for milk are best illustrated by the fact that no one has made any real study of the question and by the nature of the "points" that are supposed to indicate a good milker.

Beef cattle have been wonderfully developed within the last century but, if anything, the milk yields of cattle have declined; they have certainly not improved.

It does not seem to have struck anyone that while the eye, and the "touch" or "feel" of the skin, were quite good guides as to the flesh and fat that an animal developed, there was a better standard for dairy cattle in the milk yield. But in order to utilise the yield as a standard to which to breed, it is necessary to weigh the whole yield of every cow and her heifers for some years. This means no little trouble and attention. Moreover, it means steady trouble twice a day regularly.

The milk record kept for these experiments has been maintained without a single break since the beginning of 1904. Not one single milking has escaped record.

The butterfat estimations have been as regular since 1905. At first tests were made for every milking, but as this was found to be too expensive both in money and time, a sample is taken at every milking for each cow and the combined sample is tested regularly every Friday afternoon; the Gerbers method being used.

This ensures as correct a record as is possible of each cow's performance in the year.

Nevertheless, the best kept record suffers from certain imperfections that must be understood and, if possible, corrected. The amount of milk given by any cow follows two curves, the first a seasonal one, due to the time of year at which she calves, and the second a physiological one due to the date of service. The same cow calving in September will have a different seasonal curve from what she would have were she calved in April. And again the curve of yield will be different when she is put in calf in the second month after dropping a calf to what it is when put in calf in the third or any subsequent month. How far these two curves contradict each other has not been fully worked out. I have tried to do so, but once a cow has started work in any given month, one does all one can to keep her calving dates in that month so that real control experiments are rare. So far, I find that they vary a good deal while following a general law more or less closely.

A curve beginning in any of the late autumn months, say October, never rises as high as one that starts in, say March, but it keeps at a

steadier level so that I believe that in the end the cows calving between October and May ultimately yield just about the normal amount. On the other hand, cows calving in July, August and September start their physiological rise on the seasonal fall and I believe that their yield is lessened. I am aware that the Irish Department of Agriculture states the exact reverse but they do not give the evidence upon which they base their view.

Temperature has a marked effect on yield. I have come to the conclusion that the optimum lies between 50°—60° Fahrenheit. Wind direction and intensity also affects yield as does sunshine: both are to be avoided, though light is most desirable. The general character of the season, whether wet or dry (the first is to be preferred), the nature of the fodder or roots used, the skill of the milkers, the temper of the byreman, all leave their mark on the milk record, and the effect of the most transitory illness is at once visible in the amount registered.

One source of inaccuracy can be corrected more or less adequately. A cow running twelve months neat between calves gives a normal lactation, but if this period is shortened or lengthened the lactation ceases to be quite normal. Here, however, we must remember the following facts. Some cows will remain in milk for two years between calves, some will go out of milk at the end of ten months or thereby even if yield.

Some cows if run dry will give more milk than they would have, had they been put in calf, and some will give less. After much study I have come to the conclusion that the proper correction is to take the total lactation figure and divide it by the total of days between calving dates and multiply the quotient by 365. This decreases the figure of yield for the long lactations and increases it for the short ones. All the figures of yield in these tables have been thus obtained. The butterfat percentages are averages for the whole lactation.

This correction which may appear arbitrary to workers unfamiliar with data afforded by the consideration of large numbers of records is, I am convinced, a fair representation of the facts and it should be noted that while it reduces the maximum range of difference in yield, it has never occasioned the placing of good milkers in a low category nor the reverse.

The curve of butterfat exactly reverses the milk yield curve, falling as long as the milk curve rises and rising when it falls. I have only one exception to this rule, a case where the butterfat curve, if drawn, would make an almost straight line rising slightly in the second half of the

lactation period. She appears in Table II as No. 105 with 5.9% of butterfat.

In considering the facts disclosed in these tables, it has to be remembered that all our beef breeds are inbred. But as the qualities required are as often seen in the female as in the male, both sides are bred to. I append on p. 90 the pedigree (VII) of the first noteworthy shorthorn bull as a sample of breeding for beef. It causes me no surprise that highly bred shorthorns are notoriously deficient in milk. Mr Taylor produced a well-known herd of "milking shorthorns" and his pedigrees show inbreeding to male relationships.

The Jersey herd book is full of pedigrees inbred to the male though there is a tendency to use full relationships.

In conclusion, I think that the results here set out afford prima facie evidence of the direction of future breeding for an increase in milk production.

TABLE I. *Inbreeding by the Male.*

A	B	1	2	3	4	5	
Siring Bulls	Record of Bull's Dam	Number of Heifer in register	Heifer's Record		Record of Heifer's Dam		Increase or decrease in Heifer's record as compared with that of her Dam
			Gallons	Butterfat	Gallons	Butterfat	
Vaddy Erne I ...	900 4 1/2	27	450	3.5 1/2	280	3.5 1/2	Gallons 60 1/2 + Butterfat 10 1/2 + = with her Dam
Gort Sheen III ...	Not known	75	630	4.4	500	4.0	26 + 10 1/2 + 5 + 5 + 32 + 2.5 + 20 - 12 + 29 + 18 + 32 + = with her Dam
Vaddy Sheskin ...	567 4.1	69	636	4.2	51	3.8	
" " ...	"	73	660	4.0	52	3.9	
" " ...	"	83	400	4.5	54	4.0	
Vaddy Moile ...	900 4.0	61	840	3.9	650	3.3	
" " ...	"	62	660	4.0	500	4.0	
Vaddy Creggan ...	580 4.0	102	507	4.0	53	3.3	
Vaddy Burntollet	900 4.0	74	613	4.7	49	4.2	
" " ...	"	84	650	4.0	600	4.2	
" " ...	"	82	657	4.9	48	580	4.0
" " ...	"	95	500	4.5	48	580	4.0
Vaddy Burntollet II	540 4.2	113	500	5.2	74	613	4.7
Averages ...	"	"	594	4.29	"	530	3.9
Vaddy Erne III...	580 4.0	68	630	3.6	28	500	3.9
Vaddy Shannon...	500 4.0	109	270	5.0	83	400	4.5
Vaddy Burntollet	900 4.0	72	500	4.0	50	321	3.6
" " ...	"	70	700	3.8	36	650	3.3
" " ...	"	78	654	4.9	39	600	3.8
" " ...	"	86	534	4.7	52	485	3.9
" " ...	"	107	609	4.8	52	485	3.9
Averages ...	"	"	556.7	4.4	"	491	3.8
Vaddy Erne III...	580 4.0	63	650	3.6	101	550	2.9
Gort Gallant ...	Not known	32	514	3.9	13	280	3.5
Gort Sheen III ...	"	96	550	5.5	43	550	4.4
" " ...	"	64	580	3.8	33	456	4.0
" " ...	"	80	580	4.0	33	456	4.0
Vaddy Creggan ...	580 4.0	100	520	4.8	40	550	4.4
Averages ...	"	"	565	4.26	"	473	4.03

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See Pedigree I. It should be noted that 83 is the Dam of 109 in the following

Half-brother and sister by the Bull

This cow (113) shipped her calf in her 2nd year and her figure is for that year

This cow (109) "ran out" her milk to such an extent that her record is worthless
See Pedigree II

Avuncular

This is multiple breeding, i.e. breeding to several relationships by different Bulls. See Pedigree III

2nd cousins
1st cousins
5th and 5th cousins
4th and 4th cousins once removed
4th and 4th once removed
2nd once removed, 4th and 6th cousins

TABLE II.

(a) *Inbreeding to both Male and Female, the Male being the nearest.*

Siring Bulls	Record of Bull's Dam		Number of Heifer in register	Heifer's Record		Number in register of Heifer's Dam	Record of Heifer's Dam		Increase or decrease in Heifer's record as compared with that of her Dam		Breeding	Remarks
	Gallons	Butterfat		Gallons	Butterfat		Gallons	Butterfat	(gallons % + or -)	Butterfat % + or -		
Vaddy Erne IV ...	500	3.5% ₂	101	562	4.6%	63	650	4.6%	13.5% -	= with her Dam		
" " ...	—	—	97	500	4.7	65	450	4.7	11 +	"		
" " ...	—	—	99	565	4.8	32	514	3.9	10 +	23% +		
Vaddy Craggan ...	580	4.0	98	480	4.6	57	550	4.0	14 -	15 +		
Vaddy Burnfollet	900	4.0	91	550	3.8	55	384	3.5	45 +	5.5 +		
Kilmorna Duke 22nd	Not known		79	550	4.3	55	384	3.5	45 +	19 +		
" " ...	"	"	85	570	5.5	56	490	4.0	16 +	27.6 +		
" " ...	"	"	87	650	4.2	57	550	4.0	19 +	5 +		
" " ...	"	"	88	678	4.7	59	450	3.9	50 +	20 +		
" " ...	"	"	94	620	4.7	60	500	3.9	24 +	20 +		
Averages ...	—	—	—	572	4.59	—	492	4.0	16 +	14.7 +		

Mixed inbreeding to male and female. Male is the nearer relationship in every case

(b) *Inbreeding to both Male and Female Relationships, the Female being the nearest.*

Siring Bulls	Record of Bull's Dam		Number of Heifer in register	Heifer's Record		Number in register of Heifer's Dam	Record of Heifer's Dam		Increase or decrease in Heifer's record as compared with that of her Dam		Breeding	Remarks
	Gallons	Butterfat		Gallons	Butterfat		Gallons	Butterfat	(gallons % + or -)	Butterfat % + or -		
Walton Maddon	900	Not known	103	448	4.5	66	700	3.9	36 -	15.3 +		
" " ...	"	"	105	506	5.9	63	650	4.6	17.5 -	28 +		
" " ...	"	"	106	551	4.9	68	630	3.6	12.5 -	35 +		
" " ...	"	"	110	446	5.1	81	530	4.4	17 -	15.9 +		
Vaddy Erne III...	580	4.0	81	530	4.0	43	550	4.4	3.6 -	10 -		
Averages ...	—	—	—	496	4.8	—	612	4.2	18.9 -	16 +		

Mixed inbreeding to male and female. The female is the nearer relationship in every case

TABLE III.

Out or "Chance" Breeding. The Bulls are Pedigree Animals, the Cows are not.

Siring Bulls	Record of Bull's Dam		Number of Heifer in register	Heifer's Record		Number in register of Heifer's Dam	Record of Heifer's Dam		Increase or decrease in Heifer's record as compared with that of her Dam	
	Gallons	Butterfat		Gallons	Butterfat		Gallons	Butterfat	Gallons % + or -	Butterfat % + or -
Gort Desmond ...	Not known		12	333	4.2%	1	676	4.3%	50% -	2.3% -
" " ...	"	"	13	280	3.5	3	596	3.5	53 -	= with her Dam
Vaddy Erne ...	900	4.0%	26	580	4.0	2	718	4.2	19 -	5 -
" " ...	—	—	28	500	3.9	9	620	4.1	19 -	5 -
Vaddy Erne III ...	580	4.0	66	700	3.9	34	600	3.7	16 +	4.4 +
Gort Gallant ...	Not known		40	550	4.4	10	460	4.0	20 +	10 +
" " ...	"	"	41	437	4.2	14	530	3.9	17 -	7.6 +
" " ...	"	"	43	550	4.4	4	900	4.0	31 -	10 +
" " ...	"	"	45	511	4.4	16	750	4.0	31 -	10 +
" " ...	"	"	46	644	3.7	9	620	4.1	4 +	12 -
" " ...	"	"	38	500	3.9	2	718	4.2	30 -	7 -
Dromyrouke ...	"	"	14	530	3.9	8	545	3.8	2.3 -	2.6 +
Gort Sheen III ...	"	"	39	600	3.8	9	620	4.1	3 -	7 -
" " ...	"	"	54*	500	4.0	9	620	4.1	20 -	2.5 -
" " ...	"	"	67	600	4.0	9	620	4.1	3 -	2.5 -
" " ...	"	"	89	640	4.7	9	620	4.1	3 +	14 +
" " ...	"	"	30	500	3.9	2	718	4.2	30 -	7.6 -
" " ...	"	"	52	485	3.9	2	718	4.2	32 -	7 -
" " ...	"	"	31	500	3.5	14	530	3.9	5.6 -	11 -
" " ...	"	"	53	500	3.3	8	543	3.8	7.9 -	12 -
" " ...	"	"	51	550	3.8	11	585	4.5	5.8 -	18 -
" " ...	"	"	37	500	3.8	15	788	4.0	36 -	5 -
" " ...	"	"	60	500	3.9	22	756	4.1	40 -	5 -
" " ...	"	"	36	650	3.3	18	800	4.0	23 -	26 -
Vaddy Sheen ...	585	4.5	48	580	4.0	15	788	4.0	36 -	= with her Dam
" " ...	—	—	49	600	4.2	22	750	4.1	20 -	2 +
Vaddy Moile ...	900	4.0	56	490	4.0	23	570	3.9	10 -	3 +
" " ...	—	—	57	550	4.0	11	585	4.5	5.8 -	12.5 -
" " ...	—	—	59	456	3.9	20	600	4.1	25 -	5 +
Vaddy Burntollet ...	900	4.0	93	488	3.7	16	750	4.0	35 -	7 -
" " ...	900	4.0	76	570	3.9	34	600	3.7	5 -	5 +
Averages ...	—	—	—	528	3.9	—	655	4.03	19.4 -	3.2 -

* See Pedigree VI.

TABLE IV.

(1) *Annual Average of Butterfat for the whole herd.*

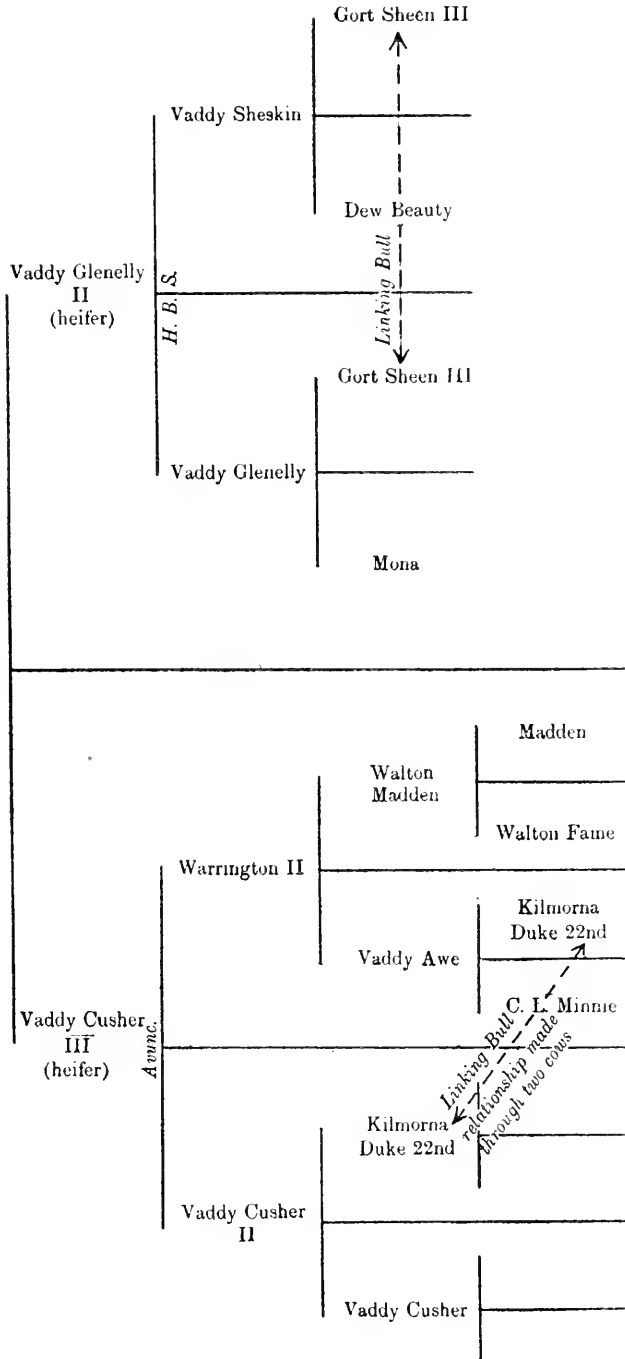
1905	4.1%
1906	3.9
1907	4.05
1908	4.04
1909	3.97
1910	3.97
1911	3.94
1912	3.99
1913	4.0
1914	4.04
1915	3.97
1916	4.33
1917	4.94
1918	4.85
1919	4.85

(2) *Percentage increases of successfully bred Heifers compared with their Dams, expressed in averages for the whole herd.*

Yield of Dam	Increase per cent. in Heifer
Under 300	77% +
Between 300 and 400	47 +
" 400 and 500	16 +
" 500 and 600	14.8 +
Over 600	7.6 +

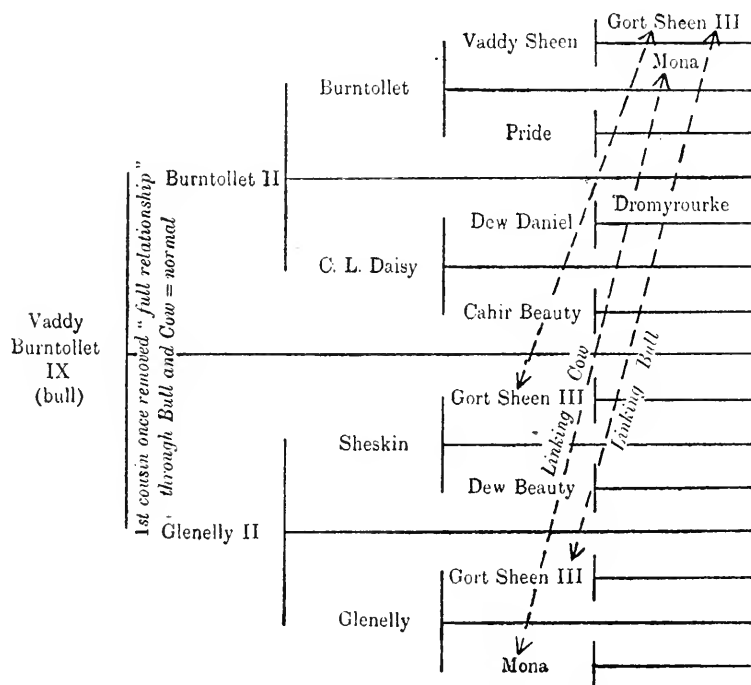
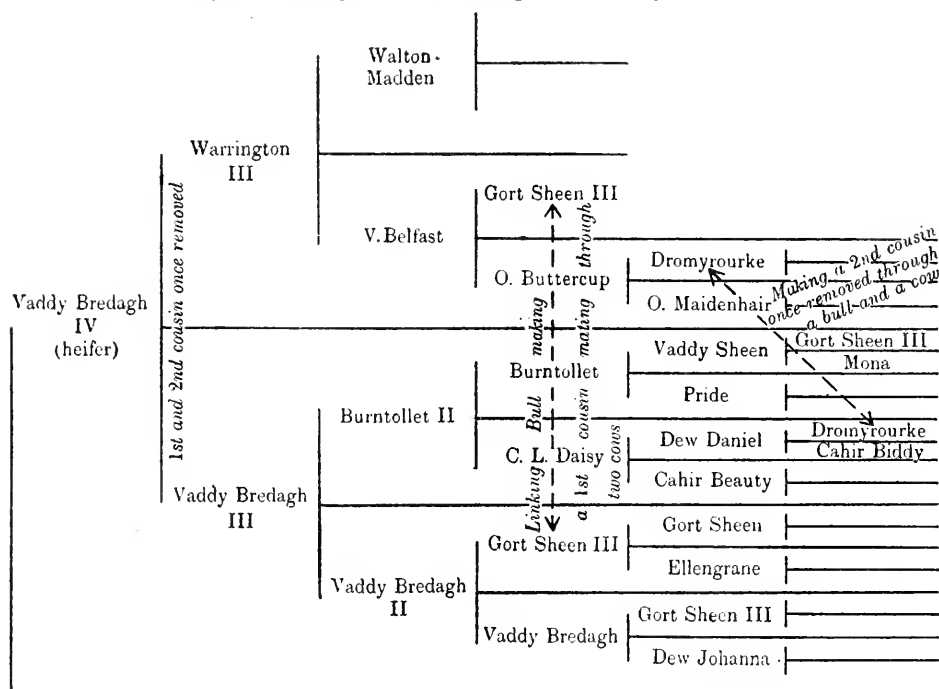
Yield of Dam in Butterfat	Increase per cent. in Heifer
3 — 3.5%	13.2% +
3.5—4	23 +
4 — 4.5	8.6 +
4.5—5	8.47 +

*Pedigree No. I to illustrate Half-brother and sister (= HB and S) mating.
Also a "normal" mating, i.e. one passing through a bull and a cow sired
by the same bull.*



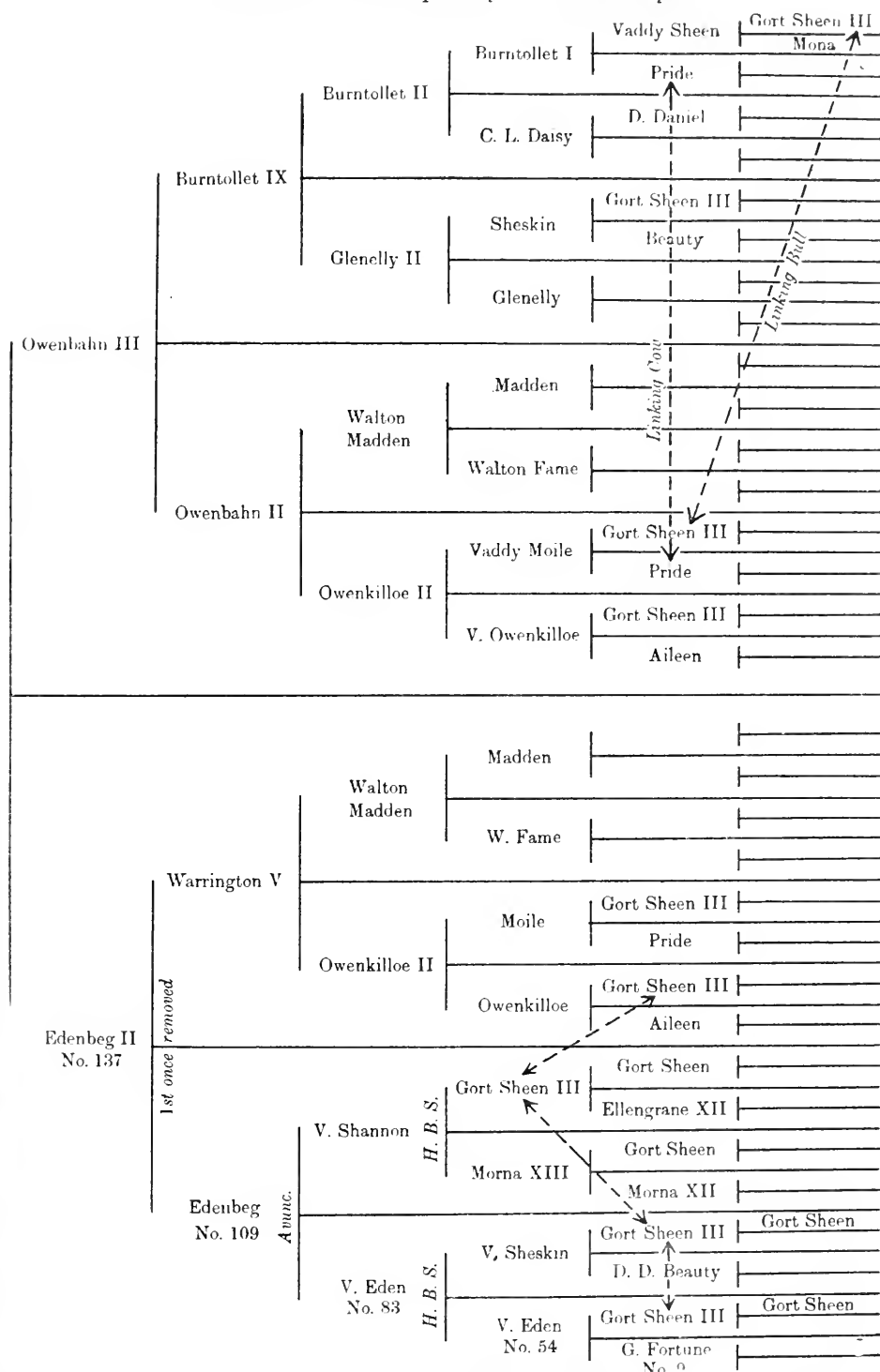
*Pedigree No. II to illustrate avuncular mating and also showing the link
passing through two cows daughters of the same bull.*

Pedigree III illustrating first cousin mating and a second cousin once removed, therefore showing a case of multiple inbreeding to the male.



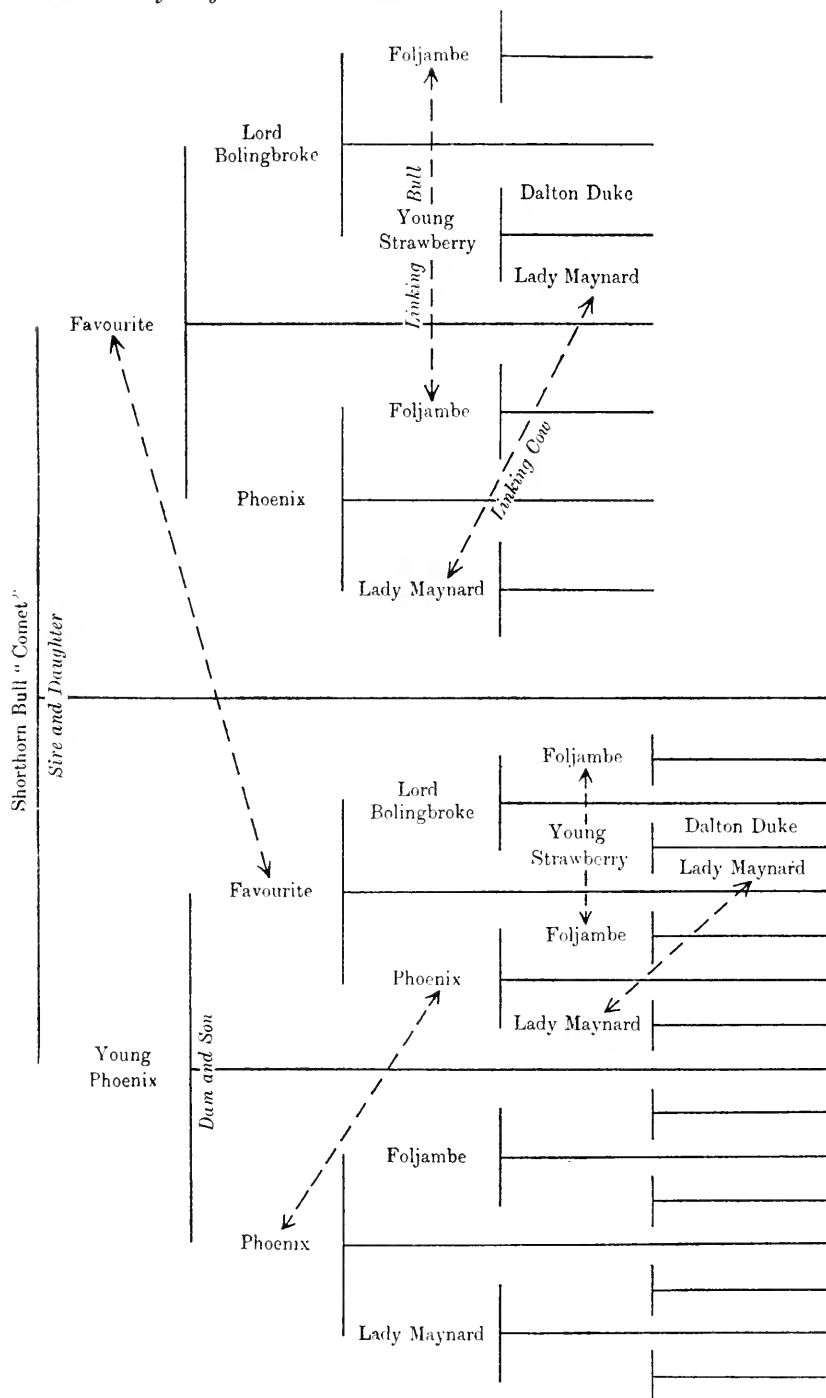
Pedigree IV illustrating a "full relationship" with bull repeated in the cow's pedigree.

Pedigree V illustrating a "nearly full" relationship that seems to be of much the same value as a quite "full" relationship.



Pedigree VI an unsuccessful strain so far. No. 109 ran her milk out so that no real record could be kept. No. 137 has calved recently; she is more promising.

Pedigree VII. Shorthorn Pedigree quoted from Wilson's "Evolution of British Cattle." There are six generations and only three bulls: Foljambe, Dalton Duke and the Sire of Lady Maynard, and three cows: Lady Maynard and the dams of Foljambe and Dalton Duke.



ROOT-CUTTINGS AND CHIMAERAS II.

By W. BATESON, M.A., F.R.S.

(With Plates XIII and XIV.)

Bouvardia.

IN a former paper¹ I recorded the production of the red-flowered variety Hogarth from the roots of *Bouvardia* Bridesmaid which has pinkish white flowers. This behaviour is perfectly consistent. At various times we have raised from Bridesmaid 29 root-cuttings (besides others not counted), which in every case bore Hogarth flowers. Very rarely a streak or flake of pinkish white has occurred on these flowers such as I have seen on other varieties of *Bouvardia* (e.g. Cleveland and Lemoinei) but they are exceptional. Perhaps one or two such flakes are seen in a season among our collection, and they do not come with any special frequency on the derived Hogarths.

From Hogarth *ex* Bridesmaid's roots 64 root-cuttings have been raised, all Hogarth *except one which was Hogarth colour but single-flowered*, whereas Hogarth and Bridesmaid are fully double. This single had anthers which dehisced containing much pollen, in microscopical appearance all bad. Singles arising as root-cuttings from double Bouvardias have often been recorded in literature, especially from Alfred Neuner, but this is the only instance observed here. A. Neuner has only given us three root-cuttings which have flowered as yet, both double, exactly like the parent plant.

From Hogarth *ex* Hogarth *ex* Bridesmaid 63 normal Hogarth have been raised as root-cuttings and from these again have come 13 normals.

From the *single* Hogarth (*ex* H. *ex* B.) we have raised 6, all singles like the immediate parent.

The following kinds have given root-cuttings which on flowering were exactly like the parent:

- A. Neuner, white double (3).
- elegans, scarlet single (15).

¹ *Journ. of Genetics*, 1916, Vol. VI. p. 75.

Humboldtii, white single, glabrous (23).

jasminiflora, whitish pink (1).

King of Scarlets, scarlet single (12); and from these again (7).

Lemoinei, red double (25).

Pres. Garfield, pinkish white double (2).

Priory Beauty, rose single (3).

The Bride, white single (2).

Vreelandii, white single (10).

leiantha, a species, scarlet single (9).

and from a seedling, scarlet single, produced by the late Mr Allard from Cleveland \times *leiantha* (2).

Vulcan, a scarlet single, short-styled, gave 27 root-cuttings like itself and *one rose-pink single*¹.

President Cleveland, scarlet single, long styled, gave 23 true to type, and 8 peculiar, having flowers scarlet marbled with white. These flowers were rather smaller and looked unhealthy, but for several seasons they have kept the same character, and the plants seemed in normal health. The margins of the petals are scarlet, and the marbling consists of whitish lines irregularly distributed over the petals, coalescing towards the central and basal parts. In the streaks the substance of the petals is somewhat thinned, a feature which gives them a depauperated appearance. Our stock of Cleveland came from two commercial sources, and the two lots were not kept distinct. It is therefore doubtful whether both kinds of root-cuttings came from one plant in this case.

From roots of true Cleveland *ex* Cleveland 21 were raised all true; and from them again 7 all true.

From roots of marbled root-cuttings of Cleveland we had 16 marbled, 11 with slight and irregular traces of the marbling, and one *not* marbled, being true Cleveland.

A variegated form of Humboldtii, having a green core and a pale yellowish green cortex, gave 2 root-cuttings green, as might be expected. These have not yet flowered.

In style-length the root-cuttings have always agreed with the parent plant, shorts coming from shorts and longs from longs.

Pelargoniums (Fancy).

Fancy and especially "Regal" (i.e. semi-doubles with petals crumpled) *Pelargoniums* have been said to give root-cuttings with flowers differing

¹ Though this "sport" came alone there is no reason to doubt that its origin was correctly recorded. We had no similar variety.

from those of the parent plant. This has been observed in three cases.

Escot (Pl. XIII, fig. 1) has flowers white with a large purplish red blotch on each petal. It is characteristic of the variety that the petals, especially the two dorsals, roll back more or less. A plant gave off a natural "sucker" (from a root) which bore flowers as shown in Pl. XIII, fig. 2. They are larger than type (70 mm. across the largest flower against 62 mm. in the parent); and flat, showing no disposition to roll back. The peripheral areas of the petals are pinkish, not white, and the blotches much redder than those of type, a feature insufficiently rendered in the coloured figure as reproduced. A root-cutting has since been raised from Escot, and its flowers agree with those of this sucker. The rolling-back of the petals in the parent is perhaps due to strain produced by the greater size of the flower proper to the included "core." The root-cuttings are somewhat taller than the type.

Mrs Gordon has flowers white and pink as shown in Pl. XIII, fig. 3, with guide-marks of the dorsal petals only lightly represented. Three root-cuttings are all alike (Pl. XIII, fig. 4), have much more colour, a full pink, on all petals, and in addition deep crimson guide-marks. These root-cuttings are very like and probably identical with the variety called "Cardiff." Both type- and root-forms may have more colour than appears in the figures, especially in newly opened flowers, but the relative amounts of colour are correctly represented. In Mrs Gordon the guide-marks are only distinguishable as "ghosts."

Pearl is a white semi-double Regal (Pl. XIII, fig. 5) having small and evasive purple patches in the area of the guide-marks. Sir W. Lawrence kindly gave me a plant of Pearl having a large branch with flowers heavily marked with red (Pl. XIII, fig. 6) much as in the varieties known as Mme Thibaut and Emmanuel Lias (? synonymous). Three root-cuttings raised from Pearl all have exclusively flowers of this coloration. Doubling in parent and the root form is similar in degree. Pearl itself has been grown here on a fairly large scale. At various times three flowers have been produced by it with a patch of red as shown in Pl. XIII, fig. 7. These patches must be regarded as indicating a break through of the underlying tissue, like the green patches so often seen on the leaves of some variegated chimaeras composed of a white cortex overlying a green core.

The three examples mentioned are the only cases in fancy Pelargoniums of root-cuttings differing from parent plants up to the present. Numerous varieties have been tried, but at first we were not very successful in raising such plants. The technical difficulties have now

been largely overcome, and we have a large series which will flower in due course. Plants identical with the parent have been raised from Lady Doreen Long (1); Queen Alexandra (1); Kingston Beauty (several); and from Touchstone, a scented-leaved *Pelargonium* (12).

Pelargonium (Zonal).

Though no root-cutting has yet been raised from it the properties of a salmon, fringed zonal raised by Messrs Jarman and by them called "Golden Flame" (Pl. XIV, fig. 1) should be considered here. The leaves of this variety are shiny, stiff and crumpled or buckled. Its flowers have lacinated petals and are devoid of functional female organs, the pistil being reduced and the ovary aborted. The anthers are normal, containing abundant and good pollen. The plant is therefore a male. Upon these plants not rarely a shoot arises which has leaves flat, with a dull matt surface like that of most leaves of zonals. On such shoots the flowers are normal hermaphrodites, and the petals are entire. Occasionally leaves otherwise of the characteristically crumpled kind have areas, small or large, of the sport variety.

Miss Cayley has supplied the following notes on the differences in structure between the two kinds of leaves:

Macroscopic Characteristics of Leaves.

				Type (shiny)	Sport (dull)
1.	Surface, upper	...		Shiny	Dull
	ditto lower	...		Dull	Dull
2.	Size of leaf	...		Smaller	Larger
3.	Shape	Somewhat ivy-leaved: crumpled	Typical zonal leaved: flat
4.	Lobes of leaf	...		More acutely pointed	Rounded and more obtuse
5.	Substance of leaf	...		Stiff	Soft
6.	Hairs, upper surface	...		Numerous, but fewer than on the "sport"	More numerous than on the "type"
				Somewhat erect	Markedly bent towards the periphery of the leaf
				Thinner than the sport, but slightly longer	Somewhat coarser
7.	Hairs, lower surface	...		Somewhat erect	Not so markedly bent, much the same as on the "type"
8.	Petiole	Stiff	Less stiff
				Shiny	Dull
				Somewhat shorter	Longer
				Hairs less coarse but erect	Hairs coarser but erect

Microscopic Characteristics of Leaves.

			Type	Sport
1.	Cuticle	...	4—5 μ thick	2—4 μ thick
2.	Surface of upper Epi-dermis		Flat. In section the outline is straight except at bases of hairs	Irregular: in section outline wavy
3.	Surface of lower Epi-dermis		No clear difference: somewhat wavy in outline	

TABLE—*continued*.

	Type	Sport
4. Epidermal cells: upper	Small: <i>with both upper and lower cell-walls thickened</i>	Larger: <i>no thickening of lower cell-walls</i>
5. ditto lower	No clear difference	
6. Palisade cells ...	Elongated in vertical plane: compressed together, and regular in shape	Shorter, wider, less crowded and less compressed: more irregular in shape
7. Layers of palisade cells	Variable. 1—3 layers	Less variable: mostly one layer, occasionally more than one
8. Spongy parenchyma...	No clear difference	
9. Bases of hairs ...	Raised	More raised than in type

When shiny and dull areas exist in the same leaf all stages of transition from the typical form to the other occur very irregularly. The change from thick cuticle to thin cuticle can be fairly abrupt, but the change in the shape of the palisade cells is more gradual and very irregular. A few "sport" palisade cells can occur in areas of "type" tissue and vice versa, and the differences are not so clearly defined in the internal tissues as might be expected from the external appearance of the leaf. The fixation of the transitional parts is difficult, and no good microtome preparations have so far been obtained. The two types of tissues react differently with the same fixative; the "sport" tissue is penetrated more rapidly than the "type" tissue, and hence is fixed sooner than the "type."

The shiny appearance of the short leaf is possibly due to:

- (1) Thickness of cuticle.
- (2) Flat surface of the epidermis.
- (3) Fewer hairs which are more erect and somewhat finer as compared with the bent hairs of the sport.

The darker green appearance of the same leaves is probably due to:

- (1) Longer, more densely packed palisade cells.
- (2) Extra layers of palisade which occur somewhat irregularly.

D. M. CAYLEY.

The inclusion of cells belonging to either form within the tissues of the other is especially remarkable.

Spiraea ulmaria.

A variegated form has stems, petioles, and central parts of the leaflets devoid of chlorophyll (Pl. XIV, fig. 2), and of a whitish yellow colour. Ordinary green plants are perfectly fertile on both male and female sides, but this variegated plant is quite sterile, forming no seeds or pollen. A few ill-formed carpels have been found on it, but the seeds they contained were aborted and did not germinate. The condition is closely reminiscent of the zonal *Pelargonium*, "Freak of Nature," mentioned in *Jour. Gen.* 1919, VIII. p. 97, *note*, which has green borders to leaves and stipules and is totally sterile on both sides. The extraordinary feature of that plant is that the green, white, and green-over-white shoots which Freak of Nature often produces are perfectly fertile. The variegated *Spiraea* has not hitherto produced any shoots other than those described. From its roots it readily gives rise to adventitious buds, and all leaves borne by them are albino, quite destitute of chlorophyll, like the stalks and petioles.

In my previous article on root-cuttings I spoke of the dissimilar forms which arise as being in all probability included as "cores" within a cortex of the ostensible type. The whole plant is thus regarded as a periclinal chimaera, one variety enclosing another, and this enclosed form may be expected to come out whenever the plant makes an adventitious bud by endogenous growth. Though this view is presumably correct in most cases the distribution seen in the variegated *Spiraea* and Freak of Nature show that other possibilities must be remembered. For in these plants the white tissue is not covered in, but extends through the whole of the internodes, and doubtless the root also. The growing point alone carries up with it the power of making green tissue. In such plants as the *Bouvardia* or *Pelargoniums* which give dissimilar root-cuttings the two kinds of tissue are not recognizably distinct in the plant until they flower, and though perhaps unlikely, it is not impossible that the kind which arises by adventitious buds may really provide the *whole* of the root and perhaps the internodal regions. Many herbaceous variegated plants arranged periclinally are liable to give shoots composed entirely of either their external or their internal constituents. Such shoots with special frequency arise near the base of the plant, i.e. just above the level at which the stem was divided in propagation. Though their mode of origin is not always easy to decide, it must be supposed that they are generally produced by adventitious buds. These evidently are not always

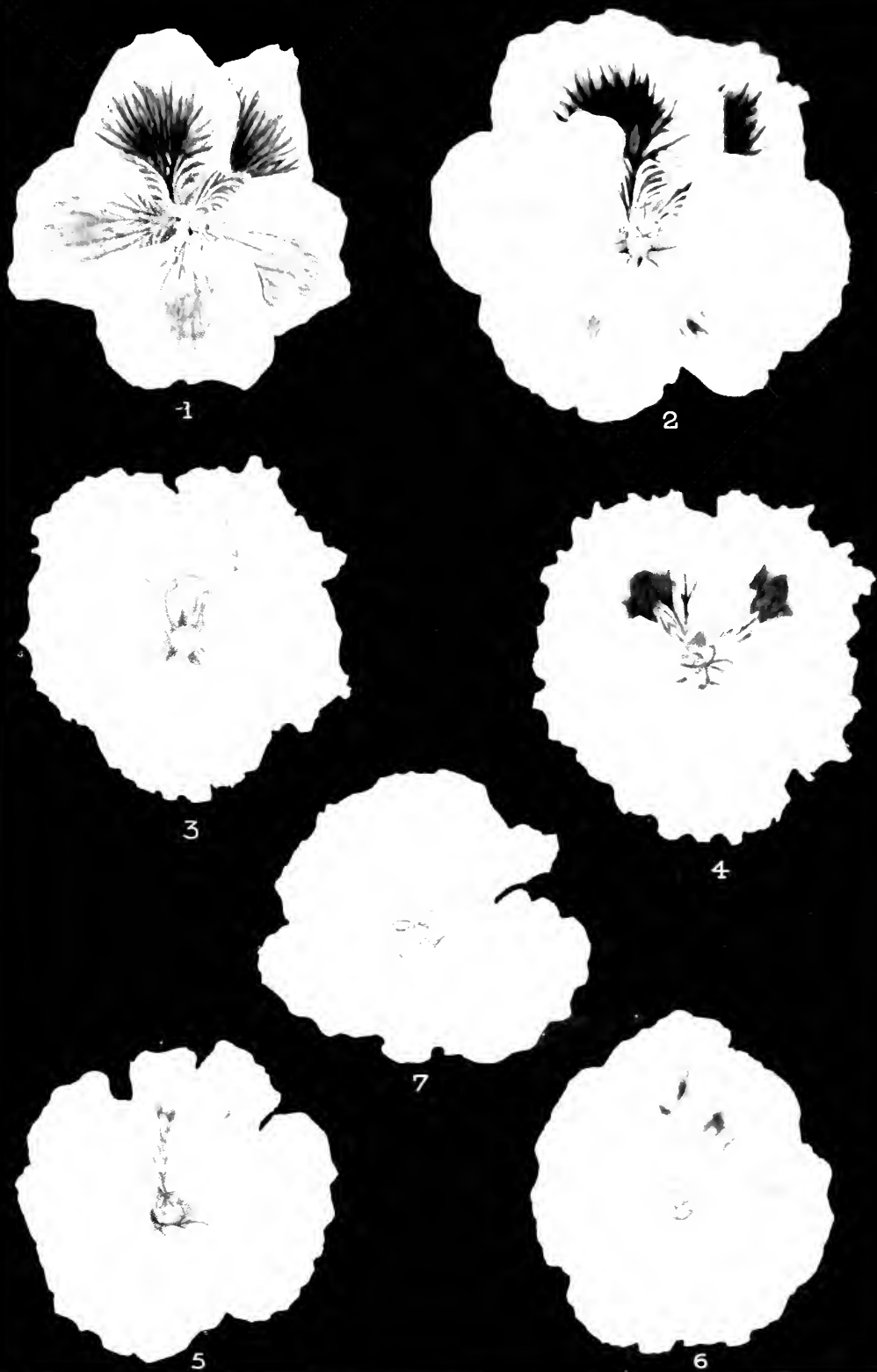




Fig. 1.



Fig. 2.



Fig. 3.

endogenous but may be originated by a periclinal division in the cortical layer.

In such an example as the crumpled zonal here described, or indeed in any periclinal chimaera with patches of its core coming out on the surface of leaves, the process by which this change is brought about is very difficult to imagine and I do not know how it may be represented. The growing point must contain both elements, but the emergence of that which is normally enclosed seems at present to be purely fortuitous.

As regards *reversals* of the layers, such as I described in *Jour. Gen.* VIII. 1919, p. 94, it is worth observing that though we have now fairly numerous cases of white-over-green turning to green-over-white, a change which in some plants happens frequently, we have not hitherto seen a single instance of the contrary. Of *Euonymus*, some zonals, an ivy-leaved *Pelargonium*, and *Arabis* we have several large and well-grown plants of the green-over-white kinds, but though occasionally the white has come to the surface in a small area, no reversal has been found on such plants. Possibly we may regard white-over-green as an arrangement mechanically less stable than green-over-white.

Several attempts have been made to breed the root-cuttings with their parent plants, an experiment offering attractive possibilities, but we have hitherto been unsuccessful.

EXPLANATION OF PLATES.

PLATE XIII.

- Fig. 1. *Pelargonium Escot*.
- Fig. 2. Root Cutting of *Escot*.
- Fig. 3. *Pelargonium Mrs Gordon*.
- Fig. 4. Root Cutting of *Mrs Gordon*.
- Fig. 5. *Pelargonium Pearl*.
- Fig. 6. Root Cutting of *Pearl*.
- Fig. 7. Flower with red blotch, a form occasionally seen on *Pearl*.

This plate is from drawings by Mr C. H. Osterstock. In the photograph the colours of *Escot* and the two forms of *Mrs Gordon* are approximately correct. In *Escot*'s root-cutting the red should be distinctly brighter, without any bluish tinge, and the same applies to the red colour in figures 6 and 7.

PLATE XIV.

- Fig. 1. Zonal *Pelargonium Golden Flame*. On the right is seen the foliage of the type, which is buckled and shiny. On the left the sport, with leaves flat and dull. The two right-hand inflorescences are laciniated. The two left-hand inflorescences bear mixed flowers, some entire, some laciniated. The fruits formed in two entire flowers are visible. These mixed inflorescences belonged to the area of transition.

Fig. 2. *Spiraea ulmaria*: leaf of variegated form.

Fig. 3. ditto leaf of normal green form.



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W. BATESON, M.A., F.R.S.

DIRECTOR OF THE JOHN INNES HORTICULTURAL INSTITUTION

AND

R. C. PUNNETT, M.A., F.R.S.

ARTHUR BALFOUR PROFESSOR OF GENETICS IN THE UNIVERSITY OF CAMBRIDGE



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NOTES ON THE GENETIC BEHAVIOUR OF CERTAIN CHARACTERS IN THE POLECAT, FERRET, AND IN POLECAT-FERRET HYBRIDS.

By FRANCES PITT.

(With One Text-figure and Plates XV and XVI.)

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I. INTRODUCTION.

These notes deal with the genetic behaviour of colour and certain cranial characters in the ferret, *Martes furo* (Linnaeus), in the polecat *Mustela putorius* (Linnaeus), and in the hybrids obtained by crossing the two species. Unfortunately, owing to the difficulty of keeping a number of flesh-eating animals, which difficulty was much greater during the War, and since then to the loss of all my ferrets from distemper, my observations and results are very incomplete. They are only published

Skull measurements to show comparative sizes in the Polecat, Ferret, and their Hybrids.

	Number	Sex	Condylar length	Zygomatic breadth	Maxillary breadth	Interorbital breadth	Rostral breadth over canines	Depth of brain-case	Palatal depth behind tooth-rows	Mandible	Maxillary tooth-row	Mandibular tooth-row	Post-orbital breadth	Observations	Locality
Ferret, No. LVI coll. F. P. ...	♂	♂	67.0	42.0	35.5	19.0	17.5	18.0	20.0	43.0	20.0	25.0	13.0	Teeth very worn	—
Ferret, No. 20	♀	58.0	35.5	32.0	16.0	14.0	16.0	16.0	36.5	19.0	23.0	13.5	Teeth slightly worn	—
„ No. 28	♀	59.0	33.0	30.0	15.0	13.0	16.0	16.0	35.0	16.0	20.0	14.0	Teeth not worn—18 months old	—
„ No. 33	♀	55.0	32.0	29.0	14.0	13.5	15.0	15.0	33.0	16.0	18.0	13.0	„	—
Polecat, No. LV coll. F. P. ...	♂	♂	67.0	40.0	35.5	19.0	17.5	20.0	20.0	42.0	20.0	24.0	18.0	Teeth slightly worn	Nr Aberystwyth, Cardiganshire
„ No. LIII	♂	70.0	42.0	38.0	19.0	17.0	20.0	20.0	42.0	20.0	24.5	18.0	Teeth worn	Tregaron Bog, Cardiganshire
„ Brit. Mus. 39. 7. 15. 3	♂	♂	66.0	40.4	37.0	17.8	16.0	20.0	18.4	40.0	19.0	23.4	—	Teeth moderately worn	No exact locality
„ Brit. Mus. 0. 10. 9. 1	♂	♂	66.8	41.4	36.8	18.0	17.4	19.6	18.0	42.6	19.4	24.0	—	„	Nr Aberystwyth, Cardiganshire
Polecat, No. XVIII coll. F. P. ...	♀	♀	61.0	35.0	33.0	17.0	15.0	17.0	18.0	37.0	18.0	22.5	16.0	Teeth worn	Nr Aberystwyth, Cardiganshire
„ Brit. Mus. 39. 7. 15. 2	♀	♀	62.4	38.0	35.2	16.8	15.0	18.4	17.0	37.0	17.8	21.4	—	Teeth slightly worn	England, no exact locality
„ U.S.A. Nat. Mus. 791	♀	♀	—	32.2	30.0	14.4	14.0	17.6	15.4	34.4	17.0	21.0	—	„	„
„ U.S.A. Nat. Mus. 792	♀	♀	61.2	35.0	31.8	14.2	13.2	17.0	16.8	37.2	18.2	21.4	—	„	„
Hybrid, No. 45	...	♂	64.0	39.0	35.0	17.0	16.0	18.0	18.0	40.0	20.0	23.0	13.0	Teeth very worn	—
Back crosses × Ferret	{ No. 29 No. 19 No. 28 No. 33 No. 26	{ ♀ ♀ ♀ ♀ ♂	{ 56.0 54.0 59.0 55.0 60.0	{ 33.0 33.0 33.0 32.0 38.0	{ 30.0 29.0 30.0 29.0 33.0	{ 15.0 14.0 15.0 14.0 17.0	{ 13.0 12.5 13.0 13.5 14.0	{ 15.0 14.0 16.0 15.0 18.0	{ 16.0 15.0 16.0 15.0 18.0	{ 33.0 32.0 35.0 33.0 37.5	{ 18.0 17.0 16.0 16.0 18.0	{ 20.0 20.0 20.0 18.0 24.0	{ 13.0 12.0 14.0 13.0 15.0	{ 18 months old 3½ years old, very worn teeth 18 months old „ Teeth worn	{ — — — — —
Back Crosses with the Polecat	{ No. 45 No. 46	{ ♂ ♀	{ 50.0 56.0	{ 28.0 33.5	{ 26.0 29.5	{ 15.0 15.0	{ 13.0 13.0	{ 18.0 17.0	{ 16.0 15.0	{ 31.0 34.0	{ 17.0 17.0	{ 20.0 21.0	{ 16.0 13.5	{ Less than half grown—milk teeth still in position Teeth slightly worn	{ — —

The Roman numerals refer to the numbers of specimens in my collection, and the Arabic to the reference figures used in my experiments. The Brit. Mus. and U.S.A. Nat. Mus. measurements are those given by Miller in his *Catalogue of the Mammals of Western Europe*.

because I am not aware of any work done on these species, and the notes may draw the attention of other workers to an interesting subject for research.

II. DESCRIPTION OF THE POLECAT AND THE FERRET.

(a) *The Polecat, M. putorius*, resembles the domestic ferret in build and general appearance. The males generally exceed 400 mm. in length (head and body), the females being smaller and averaging but 350 mm. Its most obvious superficial characteristic is its deep blackish brown colouring that has almost a plum tint, and which is much darker than the hue of the deepest of so-called "polecat" ferrets. The colour deepens into black on the underparts and extremities. The coat consists of two kinds of fur, a thick drab or yellowish wool next the skin, and a longer covering of coarse shining black hairs, which repel rain and damp. The exact hue of the animal differs according to the season and the proportions in which the two kinds of fur are present. In the winter, when the woollen under-fur is thickest and longest, the polecat appears lighter than after the summer moult. It often appears larger than its true size owing to its habit, when frightened or annoyed, of erecting its fur and fluffing out its thick tail. At the same time it makes a hissing noise, and if this attempt at intimidation fails ejects from its anal glands a most evil-smelling fluid. How disgusting an odour it is only those who have smelt it can appreciate! The polecat is highly nervous in disposition and I have never succeeded in taming one caught adult. In shape the polecat is not so light or elegant as the ferret, being somewhat more heavily built. Its head is decidedly blunter in both sexes, and, when viewed from above, forms roughly an equilateral triangle. The muzzle, tips of the ears, and a small patch of fur over each eye, are greyish white. The latter patches sometimes join to form a pale band across the face, but this is never so pronounced as in the dark form of the ferret (see Pl. XV, figs. 2 and 3). The skull is strongly built, but not more so than in the ferret, from which, however, it differs in several particulars, namely in the more flattened triangular bullae, the greater breadth of the post-orbital region, which in this species averages 18 mm. in the male, and the larger size of the carnassial teeth. Furthermore, in such polecat skulls as I have been able to examine, the ridges extending from the post-orbital processes to the sagittal crest form a much longer and more acute angle than they do in ferret skulls (see Diagram I, figs. 1 and 2). But I must add that Miller (3) figures a polecat skull with ridges forming as blunt an angle as that of any ferret's skull. The polecat ranges through Europe eastward,

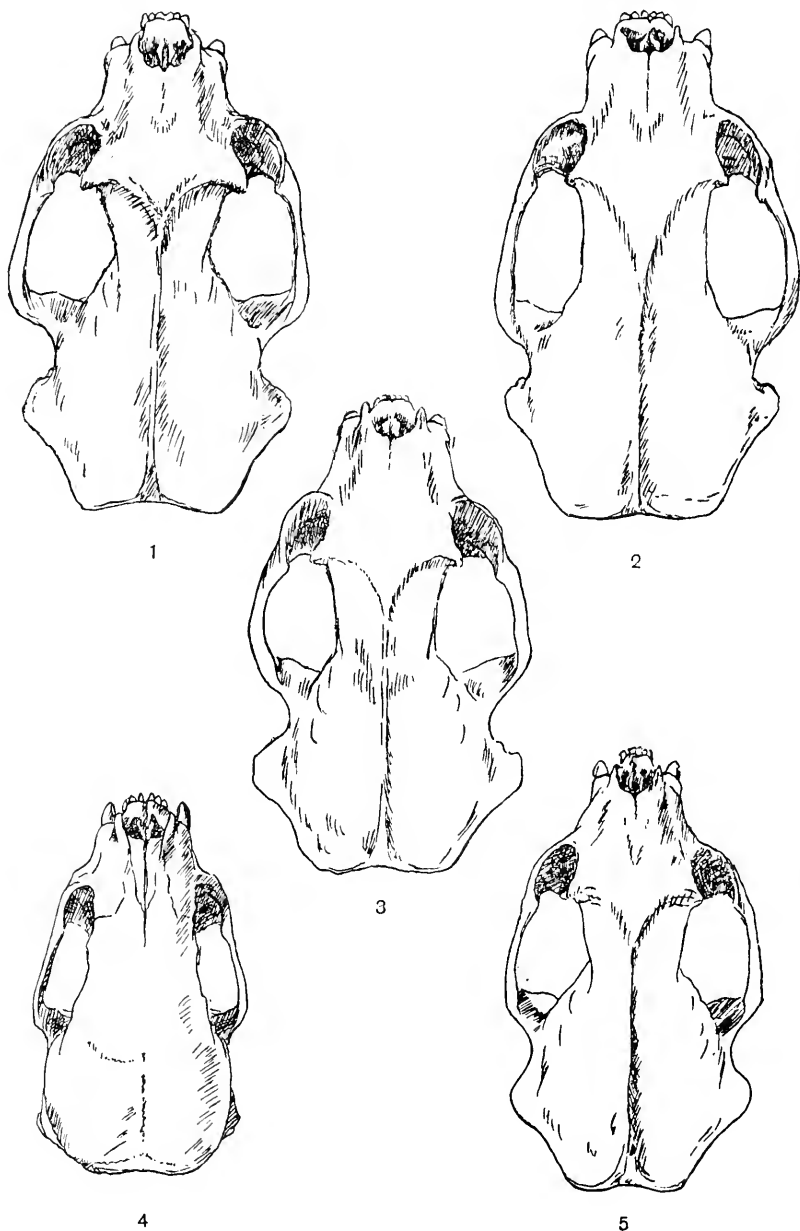


Diagram I.

1. Ferret skull, adult ♂.
2. Polecat skull, adult ♂.
3. Skull of an F_1 individual, adult ♂ No. 10.
4. Skull of No. 45, immature ♂, the produce of an $F_1 \times$ Polecat mating.
5. Skull of No. 19, adult ♀, the produce of an $F_1 \times$ Ferret mating.

and from the Mediterranean north to Scandinavia, with practically no variation, Miller describing but one doubtful subspecies from Spain, the distinguishing character of which being its more golden under-fur. In Britain the polecat is now rare, and is practically confined to central Wales. Any specimens found outside that area should be viewed with the gravest suspicion, generally proving to be merely escaped ferrets of a dark colour. The species still exists in some numbers in Cardiganshire, but how long it will be able to hold its own in the face of steady persecution is another matter.

Measurements of Polecats and Ferrets.

Number of Specimen	Sex	H. and B.	TL	Ear	H. F.	Remarks
<i>Typical dark form of the Polecat :</i>						
XVIII coll. F. P.	♀	350 mm.	127 mm.	20 mm.	56 mm.	Cardiganshire
LIII " "	♂	455 mm.	165 mm.	25 mm.	65 mm.	"
*Coll. Brit. Mus. N. H.	♂	403 mm.	163 mm.	27 mm.	61 mm.	"
" "	♂	415 mm.	190 mm.	30 mm.	62 mm.	"
" "	♀	360 mm.	140 mm.	23 mm.	53 mm.	"
<i>Erythristic variety of the Polecat :</i>						
LIV coll. F. P.	♂	450 mm.	150 mm.	21 mm.	58 mm.	"
(the above measurements are not absolutely reliable, being taken from a specimen that had been set up)						
<i>Albino Ferret :</i>						
15 " " " "	♂	358 mm.	126 mm.	18 mm.	50 mm.	—
32 " " " "	♂	375 mm.	137 mm.	20 mm.	54 mm.	—
33 " " " "	♀	312 mm.	112 mm.	16 mm.	54 mm.	—
<i>Dark Ferret :</i>						
29 " " " "	♀	371 mm.	118 mm.	21 mm.	51 mm.	—
19 " " " "	♀	312 mm.	117 mm.	20 mm.	49 mm.	—
<i>Erythristic Ferret :</i>						
20 " " " "	♀	340 mm.	130 mm.	21 mm.	53 mm.	—
28 " " " "	♀	350 mm.	117 mm.	20 mm.	49 mm.	—
<i>Hybrid Ferret-Polecat :</i>						
10 " " " "	♂	370 mm.	131 mm.	22 mm.	59 mm.	—
<i>Hybrid × Polecat produce :</i>						
45 " " " "	♂	237 mm.	68 mm.	20 mm.	42 mm.	Died young
46 " " " "	♀	340 mm.	110 mm.	20 mm.	47 mm.	—

The Roman numerals refer to the numbers of specimens in my collection, and the Arabic to the reference figures used in my experiments.

All the measurements given above were taken after death, it being found impossible to measure a live animal satisfactorily, for which reason many of those bred were never measured at all.

* From Miller's *Catalogue of the Mammals of Western Europe.*

(b) *Description of the Ferret.* It has been long assumed that *M. furo* is a domesticated form of the polecat, which it so much resembles in general build and character, the fact that the majority of ferrets are pink-eyed cream-coated albinos being considered confirmatory rather than contradictory of the idea, especially as pigmented individuals resemble polecats in their colouring and facial markings. That is to say they resemble them in their general type of marking, but not exactly, as all "fitchet"¹ ferrets I have seen have been much lighter in hue than the palest of polecats, showing, too, broader facial markings, so that there is a marked reduction of pigment compared with the wild animal. Not only are the white facial markings so much increased, but the woolly underfur, which in the polecat is invariably a buffy-drab colour, is whitish in the dark ferret. The "fitchet" ferret bears in outward appearance the same relation to the polecat that a half-printed photograph bears to the fully printed one from the same negative. The head of the ferret is narrower than that of the polecat, appearing when seen from above as an isosceles triangle, whereas the face of the polecat makes an equilateral triangle². As regards size the average ferret is a trifle smaller than the average polecat, it being a large male which exceeds 380 mm. head and body measurement. The appended table shows the respective measurements. In cranial characters we come to some important differences between the two forms, which differences have made Miller(3) express the opinion that, "the ferret, *Martes furo* Linnaeus, though usually assumed to be a domesticated variety of *Mustela putorius*, appears to be more nearly related to the Asiatic *M. evermanni* Lesson." The differing points in the ferret's skull are: the more narrow constricted post-orbital region, averaging in the male only 13 mm. in breadth, against the 18 mm. of the male polecat, which gives the skull a "small-waisted" appearance; the more inflated and less triangular auditory bullae; and the smaller carnassial teeth. The only skull of *M. evermanni* that I have been able to examine showed a marked likeness to the ferret's in all the above characters, but every ferret's skull I have seen has differed in one respect from both the single specimen of *M. evermanni*, and from every polecat's that I have met with, this character being the shortness of the ridges that proceed from the post-orbital processes towards the brain-case, and which converge at a much blunter angle than they do in the polecat. The length in seven

¹ "Fitchet" is a term commonly employed by keepers, rabbit-catchers, etc., to denote the dark or so-called "polecat" ferrets. I have avoided herein the use of the latter word for fear of misunderstanding.

² Mr A. H. Cocks first drew attention to this in the *Zoologist*, Vol. xv. 1891, p. 344.

ferret skulls averaged 14 mm., against 21 mm. in three polecats. In the *M. evermanni* skull that I examined the ridges were as long as those of the European polecat and noticeably different from those in *M. furo*. This seems to indicate a character in the ferret that is not possessed by either of the other species. In such intangible peculiarities as temperament and disposition the ferret is very different from *M. putorius*, as is shown by the ease with which it is tamed even after being neglected while young. An adult-caught polecat is quite untameable, and even half-bred ones require constant handling from their earliest youth to make them docile. It takes a very serious fright to make a placid easy-going ferret emit the vile defensive odour, but the hybrids never hesitate to make use of it. In disease-resistance too the ferret differs from the polecat, being less susceptible than the wild animal to some of the diseases met with in captivity. For instance the majority of polecats exhibited at the Zoological Gardens, Regent's Park, succumb more or less speedily to pneumonia, and I have found the hybrids nearly as delicate. In the case of epidemic diseases, such as one of the complaints that get classed under the heading of "distemper," polecat-bred ferrets have in my experience been always the first to take it, and with more fatal results than those of pure ferret descent. For instance I recently lost six ferrets in the following order: first No. 19, a dark female the offspring of a hybrid and an albino; secondly another dark female, No. 29, whose sire carried polecat blood; then a fawn ferret, No. 28, full sister to the preceding; and lastly three white ones. The latter were not only the last to take the disease, but did not succumb nearly so quickly.

From the foregoing it will be seen that there are quite a number of points of difference between the polecat and ferret, both structural, pigmental, physiological, and temperamental, so that the grounds for doubt as to whether the one is derived from the other are quite substantial, and the materials are such as to afford a most interesting subject for genetical investigation.

III. VARIATION IN THE POLECAT AND IN THE FERRET.

(a) *Variation in the Polecat.* It is noteworthy when considering the relationship of the polecat and ferret, that, as far as I can ascertain, no albino polecat has been recorded. Nevertheless it is probable such sports do occur, for unless the specimen passed into the hands of an expert and was examined as to structural details, it would almost certainly be dubbed a feral ferret. The probability is enhanced when we find that

erythristic mutations are known. In this variety the black pigment is entirely suppressed, leaving the animal a beautiful reddish colour. Erythrism is usually regarded as partial albinism, and in many species is accompanied by absence of pigment from the eyes, but in the "red" polecat the eyes are dark. The following is a good description of this mutation. "The colour may be described roughly as: under fur light buff, the longer hairy coat being a reddish-brown. When seen in sunlight the latter shows a kind of faint purple 'haze,' it is difficult to describe it otherwise." The writer, Mr F. S. Wright (4), adds that in all the specimens examined by him the facial markings were normal, "but owing to the lighter ground colour of the animal the contrast was naturally not so great as in the common dark polecat"¹. I can confirm this from my own observation.

Light brown polecats are only known from Cardiganshire, and chiefly from the district around Aberystwyth, the greater number being recorded from the neighbourhoods of Borth and Tregaron bogs. The first specimens were made known in 1902-03 (2), since when more than a dozen have been killed. From this it seems that the form has originated comparatively recently in the locality mentioned, and that the mutation (for we may safely assume it to be due to the loss of the black pigment factor) far from tending to disappear is even on the increase. As all the red polecats that have so far been recorded have been met with on the Costal Plateau of Cardiganshire, an area which extends from the River Dovey to Tregaron—about eighteen miles apart—it is evident that the area, wherein we must seek the point of origination, is a comparatively restricted one. As the first specimens were killed on Tregaron Bog it is possible that this is the locality. As would be expected in the case of a variation originating from the loss of a factor the reddish-brown colouring gives us an example of simple Mendelian inheritance. The case is somewhat interesting however, as it is not very often that we get evidence of the action of Mendel's law in wild Nature. Even in this case the information is but scanty. In July, 1915, two young polecats of the same litter, the one normal in colour, and the other red, were killed on Borth Bog, "It is noteworthy that in the two offspring the colours show no intermingling whatever" (4). Unfortunately there is no evidence to show whether the light brown type is dominant or recessive, but judging by a similar fawn-coloured variety of the ferret, presently to be described,

¹ Mr H. E. Forrest (2) has stated that the facial markings are sometimes suppressed in this variety, but he now tells me (*in litt.* Feb. 16, 1920) that he is confident it was an error due to the lessened conspicuousness of these markings on a light brown ground.

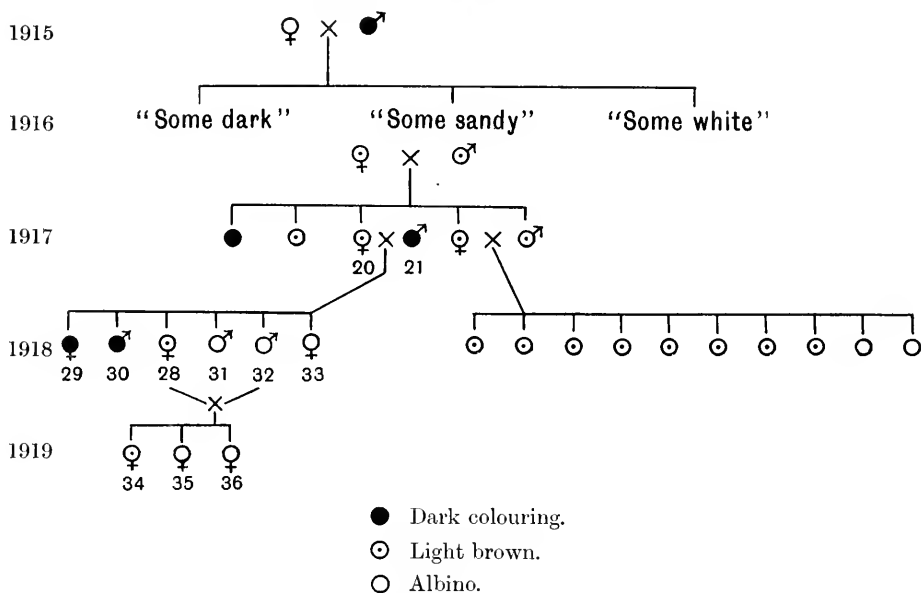
and by analogy with the behaviour of similar pigmentary characters in other species it is probably the latter. If we are right in supposing that the red coloration is due to the absence of the factor for black, it becomes at once apparent that it would be a most difficult task to decide how and when the factor first fell out. The tendency to the red coloration might lie latent for many generations until a suitable mating brought together gametes from both of which the factor was missing. It must be remembered that the dark offspring of a red \times dark mating would necessarily be heterozygotes, of the constitution $DBdB$ (I am herein using the letter " D " to indicate the dark black-brown colour, " B " the light red-brown, " db " the absence of all pigment or albinism), and if such heterozygotes are fairly widely distributed it would account for the sporadic way in which the red-brown individuals have turned up during the last seventeen or eighteen years since the first specimens were obtained. It is evident that in this variety of the polecat we have not really anything new, for the factors for it have undoubtedly been latent in the animal's constitution since it assumed its present type of coat and colouring.

(b) *Variation in the Ferret.* We may confidently assume that in the pigmented and so-called "polecat" ferret (known among keepers and rabbit-catchers as the "fitchet") we have a near approach to the ancestral type, from which the well-known white form is almost certainly an albinistic mutation. Erythristic ferrets analogous to the reddish-brown polecats are also met with, but, as the "fitchet" ferret is paler than the dark brown-black wild polecat, so is the fawn ferret paler than the "red" polecat, being much more "washed-out" looking. It is evident that we here meet with similar if not identical pigmentary characters to those found in the polecat, therefore the same letters may be used to denote the factors, D for dark black-brown or full pigmentation, B for light red-brown, and so on.

A detailed account of the behaviour of the black-brown pigmentary character will be given later on under the heading *Ferret-Polecat Hybrids*, and I will now confine myself to the erythristic variety. The exact tint of the fur is best described by the word "sandy." The colour is confined to the long outer hairs, the woolly undercoat being white. As in the red-brown polecat the absence of black pigment is correlated with size and vigour. Most of the sandy ferrets I have seen have been exceptionally fine animals. They are also noticeably quicker tempered than dark or white ones. It is my experience that they require a good deal more handling to keep them quiet and docile, and even then cannot be trusted. One sandy ferret I had was called "Ginger" on account of

her liability to snap. Other persons have expressed the same opinion to me. In connection with this it must be remembered that red-headed people are notoriously sharp tempered, and chestnut horses are often very "hot." Erythristic ferrets are not very common, but I have met with the variation in four distinct strains. The individuals that belonged to me originated from a mating between "a white female and a very large dark male...they had some dark, some white, and some sandy young ones¹." As there were several sandy young ones we may be certain that one parent, presumably the dark, was heterozygous for the red character, and that for the origin of the mutation we must go further generations back, because if the factor had fallen out at this particular mating only

Pedigree of Light Brown Ferrets.



The numbers refer to animals bred by me, and serve to identify the same individuals in different pedigrees.

one of the family could have borne the new character. When the erythristic ferrets obtained in this litter were bred from, the owner tells me, a litter of four "reds" and *one dark* resulted, which, provided no error occurred, shows that the factor for full pigmentation may be borne in a latent state by the red individuals. However the dark colouring is

¹ For this and other information I am indebted to Mr Wm. Milner, of Much Wenlock, who most kindly gave me some of his erythristic ferrets.

usually dominant to its absence, as will presently be shown when the evidence concerning the hybrids between the ferret and polecat is given. It is probable that in fawn and in "fitchet" ferrets we meet with dilution factors that complicate matters, but the numbers so far bred are too small for the facts to be elucidated. The various matings of which I have records in which fawn-coloured ferrets have been involved are tabulated below. It will be seen that in a cross of red \times dark the white class was larger and the red smaller than expected.

Tabulated results obtained from matings of erythristic ferrets:

		Dark		Fawn		Albino
Fawn \times fawn	...	1	:	4	:	0
		0	:	8	:	2
Totals		1	:	12	:	2
Fawn \times dark	...	2	:	1	:	3
Fawn \times white	...	0	:	1	:	2

IV. FERRET-POLECAT HYBRIDS.

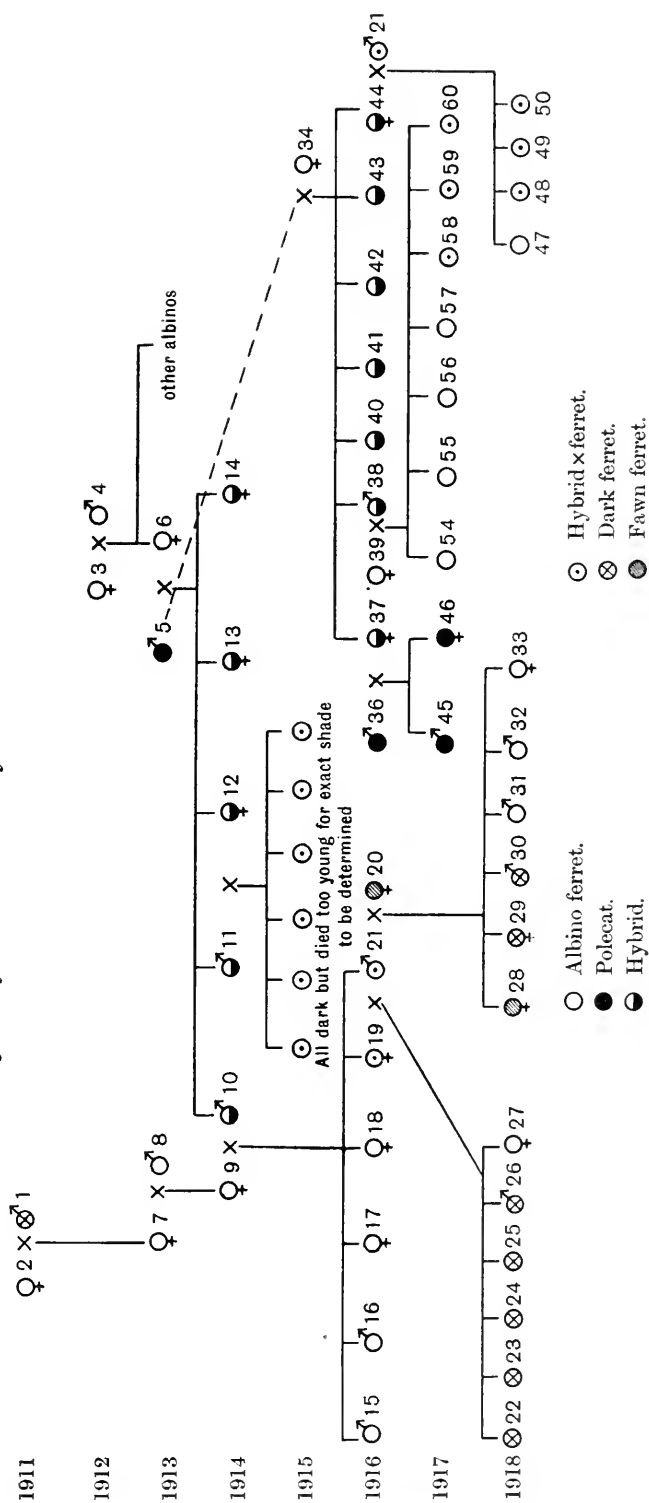
(a) As the characters in which the polecat and the ferret differ have already been described, it is unnecessary to go over them again; I will only remind the reader that they consist of certain cranial peculiarities and of coat colour. There is also considerable difference in temperament, the domestic animal being placid and easy-going, the wild one very much the reverse.

(b) In 1912 I was fortunate in obtaining a very fine male polecat from Cardiganshire, also a female, but as she never bred she is only mentioned here because she served as a standard with which to compare the female hybrids that were subsequently reared. The male, No. 5 in the accompanying pedigree (p. 111), was mated with an albino ferret of known pure white ancestry for several generations. The resulting litter numbered five, two males and three females, all dark in colour, and showing complete dominance of the wild type in the F_1 generation. Perhaps the words "complete dominance" need qualification, for, notwithstanding the hybrids were much darker than any so-called polecat ferret, they did show slight traces of the ferret side of their ancestry, inasmuch they had whitish under-fur instead of the buffy-grey wool of the true polecat. Nevertheless they were very dark in colour, the black-brown of the long hairs having the slight purplish sheen so characteristic of the polecat. The polecat temperament too was fully apparent, for, despite the fact they were made great pets of, and were constantly handled, they were

far more nervous than ordinary ferrets. They were easily frightened, and when startled would emit the horrible odour from the anal glands that constitutes one of the defences of the polecat. I have only known a ferret do this under stress of great fear and excitement—e.g. when pounced upon by a terrier in mistake for a rat! They also hissed at the least thing. They were far quicker and had more vitality than ordinary ferrets, romping and dancing together in the most delightful manner. When used for rabbiting they proved almost too quick, for it was quite difficult to pick up the nimble females as they darted in and out of the holes. They were deadly workers, killing their rabbits in a few seconds by biting them over the eyes, but never behind the ears after the manner of a stoat. A male (No. 10) was a good ratter, and I have seen him chase a rat that had bolted in the open. He was a great pet but had some undesirable traits in his character, his genius for escaping from all descriptions of cages being extraordinary. He would bite and tear his way through wire netting in a very short time, an ordinary wooden cage never kept him at home for long, and the only place where he was really safe was a loose-box with a strong well-fitting door. In his old age he climbed over a four foot pig-sty wall, made his way into a fowl-house, and therein slew six cockerells. When he died at four years old his teeth were the worn stumps of a very old animal. It then also transpired that though so polecat-like in appearance and behaviour his skull was that of a typical ferret. When placed side by side with the skull of a ferret of pure ferret ancestry it resembled it in all respects, being distinguishable at a glance from that of a polecat. Here we have an interesting case of the colour and temperament of one parent, and the cranial characters of the other, being dominant in the F_1 generation.

(c) *Notes on the Development of the Young Hybrids.* Before going on to another litter of hybrids it may be worth while to give details of the growth and development of the first family. They were born on June 26th, 1912, and on July 10th two crawled out of the nest, being then covered with milk-white hair¹, so short that their greyish-blue skin showed through it. Their mother dragged them back into the nest at once. At 17 days old they had grown a great deal, were darker, and had traces of the typical polecat facial markings. At 24 days old they were much browner, but with yet a mane of "skim-milk" coloured hair down the neck. The largest males' eyes had begun to open, and they were all

¹ Young ferrets, whether dark or albinos, and likewise young polecats, have a white baby coat. They are born naked, but quickly grow a scanty covering of milk-white hair, which as described above then gives place to the dark fur.

Diagram of the Inheritance of Colour in Ferret × Polecat Crosses.

trying to eat rabbit meat. The 25th day found two able to see a little, and all making vigorous efforts to eat. By the 36th day they were quite dark in colour, with white tips to their ears, white muzzles, but the light patches on the sides of the face as yet shadowy and indistinct. At seven weeks old they were perfect little polecats as far as outward appearance went, and it was not until they had gained their winter pelage that some slight trace of the ferret side of their pedigree could be discerned.

(d) *A Second Litter of Hybrids.* In 1916 the male polecat No. 5 was mated with another white female ferret (No. 34). She had by him a family of eight, all dark, but being a bad mother only reared three. These were in all respects exactly like the first hybrids, being quite as polecatlike in appearance, and even more nervous, for they did not get so much handling and petting.

(e) *Reciprocal Cross.* The reciprocal cross could not be made, as the female polecat which I had obtained after so much trouble never bred; but as albinism is invariably recessive to full pigmentation, we may be fairly confident that the result would have been the same.

(f) *F₂ Generation.* Owing to one mishap and another no *F₂* litter was reared to maturity. The *F₁* females that I kept to breed from caught distemper and died, but a male and female that I had given to Mr Riley Fortune did well until just before their young were born. The female then escaped from her cage, found a hole under the greenhouse floor, and there made a nest, in which her family was born. Mr Fortune kindly sent me full particulars of the progress of the litter, but misfortune was again in store, and the mother getting away was lost before her young ones could see. When deserted they were a whitish colour. As the young of all ferrets, whatever their ultimate colour is to be, have a white baby coat, this is no indication as to what they would have been like when adult. But one thing was proved, namely that the hybrids are perfectly fertile *inter se*.

(g) *F₁ Generation × the Ferret.* A mating between a *F₁* male and a white ferret (Nos. 9 and 10) gave four albinos to two dark young ones. These latter were not so dark as their sire, and approached the ordinary fitchet ferret type. Another mating of an *F₁* male with an albino female (Nos. 38 and 39) gave four whites to three darks. The total for the two litters was eight to five, whereas expectation was equality, but the numbers are too small for one to be able to arrive at any conclusions. When an *F₁* female, No. 44, was mated with a male bred from the

$F_1 \times$ albino ferret cross (No. 21), which was polecat coloured, and therefore presumably heterozygous in constitution, three dark and one white young resulted (Nos. 47 to 50)¹. When two second-cross ferrets, Nos. 19 and 21 (i.e. the produce of the F_1 generation \times albino ferrets), were bred together they had five dark young ones to one white. A mating of interest was that which has already been referred to between Nos. 20 and 21. The former was an erythristic female, the latter a dark male, the produce of a hybrid \times a white ferret. The alliance between Nos. 20 and 21 gave rise to two dark, one red, and three white ferrets. As regards cranial characters, all skulls that I have been able to examine of these hybrid \times ferret crosses have been indistinguishable in every particular from those of pure-bred ferrets. Full details and measurements of these skulls will be found in the table on p. 100.

(h) F_1 Generation \times the Polecat. In 1916 I was fortunate in obtaining another fine male polecat from Cardiganshire. He was mated with No. 37, an F_1 female by my first polecat. Her litter only numbered two. These two youngsters appeared true polecats in every respect, having the broad faces, dark coats, drab under-fur, and highly nervous dispositions of the wild animal. I subsequently found that in cranial characters too they were polecats, for their skulls were typical of *M. putorius*. The male died young, but the female lived to be eighteen months old, when she too unfortunately succumbed to pneumonia without having bred. This susceptibility to pneumonia is a characteristic of the wild animal, most captive polecats sooner or later dying of it. Pure-bred ferrets appear to be much more resistant to the disease. In temperament and disposition this young female was quite the wild animal, she was intensely nervous, bit whenever she got the opportunity, and in her excitement was always ready to emit the horrible polecat smell; in short there was no trace of the ferret about her.

(i) *Weakening of Pigmentation in Hybrid \times Ferret Crosses.* Before glancing back over the evidence that has been presented concerning polecat \times ferret hybrids, it may be as well to draw attention to the weakening of pigmentation that occurs when the polecat-ferret hybrids are bred back to the ferret, the three-fourths ferret offspring being much paler than the first cross. These individuals are very like the ordinary "fitchet" ferret, but still further dilution takes place when another back cross is made. After this the pigmented individuals are very "washy"

¹ For information concerning this litter I am indebted to Mr Owen of Oswestry into whose possession the parents had passed.

in appearance and exactly like the average dark ferret. Whether there is a true dilution factor involved appears doubtful, the lighter appearance of the animal being due to a smaller quantity of dark hairs in its coat, not to reduction of the pigment in the hair, as in "dilute" mice, rats, and rabbits. Were true dilute ferrets to occur I should expect them to be a pearl-grey colour. In "fitchet" ferrets the lighter colouring, lighter that is by comparison with polecats and their hybrids, is due to the white or pale cream under-fur, to the cream basal portion of the longer hairs, and to the general increase of cream coloured fur.

V. RECAPITULATION AND CONCLUSION.

Attention has been drawn in this paper to the interesting material for genetic study that is to be found in the polecat and ferret, the two forms have been described, together with their points of difference and resemblance, and it has been shown that the characters in which they differ are such diversified ones as coat colour, cranial peculiarities, and temperament. The doubt as to whether the ferret is a descendant of the European or Asiatic polecats has been alluded to, and evidence has been given that it at any rate will cross freely with *M. putorius*, the hybrids being fertile *inter se*, and with either parent. The F_1 generation shows complete, or very nearly complete, dominance of the polecat type as regards outward appearance, but what evidence is to hand indicates that in cranial characters the ferret is dominant. When the hybrids were bred back to the ferret the polecat coloration and temperament were soon lost. Likewise when the hybrids were bred back to the polecat, animals that were apparently pure polecats resulted. An interesting result of the back crosses with ferrets (albinos) was the gradual weakening of the colour in the pigmented offspring, due not to dilution of the pigment in the hairs, but to a reduction in the amount of dark fur. Attention has also been drawn in this article to the erythristic varieties of the polecat and ferret, and particulars have been given of the occurrence of "red" polecats in the Aberystwyth district, together with some evidence that this mutation has appeared comparatively recently, and is inherited according to Mendel's law. In the case of the ferret it is shown that erythrism is certainly dependant on a Mendelian factor, being dominant to albinism and recessive to the black-brown coloration. Both in the ferret and polecat erythrism seems to be correlated with increased size, and certainly in the ferret is usually accompanied by a quick temper and general increase of vitality. To the writer the most



Fig. 1. F_1 Ferret-Polecats at eight weeks old.

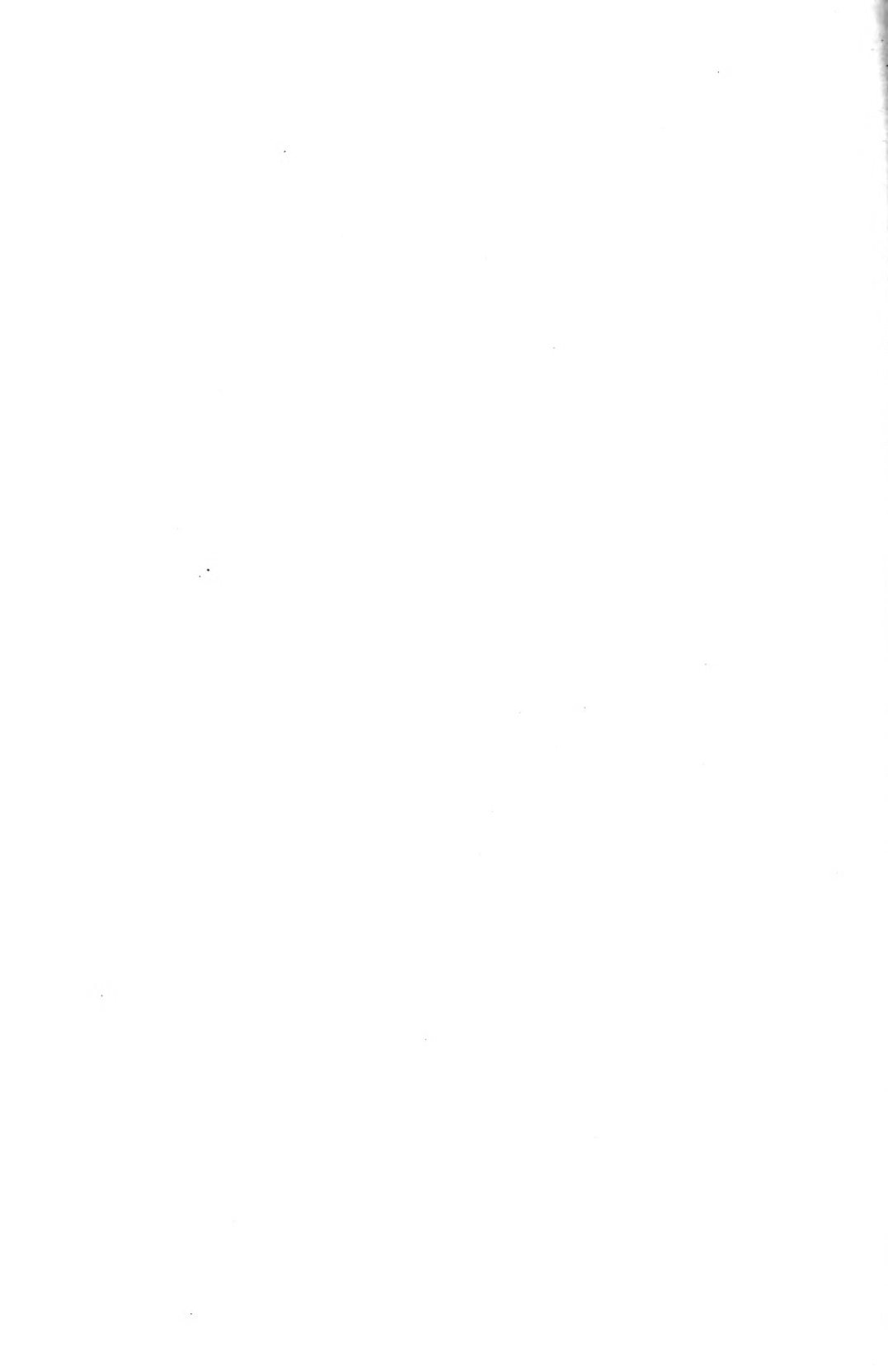


Fig. 2. Polecat (♂) from Cardiganshire.



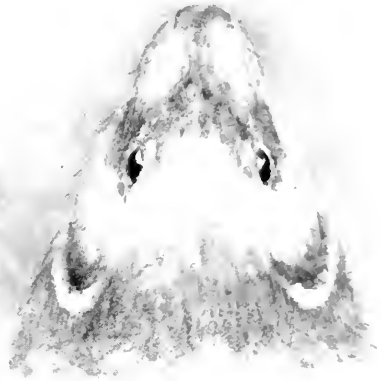
Fig. 3. Dark coloured ♂ ferret.

All the above photographs are from life.





1



2



3

1. Head of Polecat ♂.
2. Head of Ferret ♂.
3. Head of F_1 ♂.



important points that have been brought forward appear to be the indication of the Mendelian inheritance of a structural character (type of skull), and the evidence concerning a variation due to the loss of a factor appearing and maintaining itself in a state of Nature—i.e. the erythristic polecats of Cardiganshire.

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SOME EXPERIMENTS ON THE ORIGIN OF NEW
FORMS IN THE GENUS *HIERACIUM*
SUB-GENUS *ARCHIERACIUM*.

BY C. H. OSTENFELD.

Landbohøjskolens Botaniske Institut, Copenhagen.

(With Plates XVII and XVIII.)

In earlier papers (1906, 1910, 1912) I have shown that within the subgenus *Pilosella* of the genus *Hieracium* new forms arise by means of hybridization associated with apogamy. That is to say: hybridization produces the new forms (hybrids) and apogamy keeps them unaltered from generation to generation.

In the other big subgenus *Archieracium* of the same genus the matter seems different. Most of the forms are purely apogamic and only very few are sexual. Amongst the latter is *H. umbellatum*, and it is interesting to know from Mendel's letters to Nägeli, published by C. Correns (1905), that Mendel had succeeded, by using this species as father, in producing two hybrids, the only ones produced experimentally within *Archieracium*, at least as far as I am aware. As regards another sexual *Archieracium*, *H. virga aurea*, I have observed that the offspring from an individual which stood unprotected in my cultures showed distinctly the influence of hybridization as it was very heterogeneous in its appearance.

With the exception of these few cases genuine hybrids amongst *Archieracium* are not known, as we cannot rely upon the records of hybrids given in floristic and systematic literature. Mendel complains that it is "*sehr schwierig die Selbstbefruchtung aufzuhalten*" (according to our present knowledge we have to replace the word "*Selbstbefruchtung*" by "apogamy"). All my own experiments have hitherto been fruitless.

Meanwhile, as we find abundant polymorphism within this subgenus, we must search for other explanations for it. The many forms—microspecies we may call them—are apogamic and constant, the offspring being like the parent.

It seems quite natural to suppose that these microspecies are not very old, nor all of the same age. Species of a wide geographical range

are probably old, species of a restricted range may be old or may have newly arisen. In the former case they are to be considered as dying-out species and have usually a rather isolated position from a systematical point of view; the *Archieracium* microspecies can scarcely be included in this category. They must most naturally be considered as newly arisen species of restricted range.

A Swedish botanist, G. Samuelsson, has in a paper (1910) given the geographical range of some *Hieracia* from the middle of the Scandinavian peninsula. He shows that some of them have a very restricted area of occurrence, mostly with a centre where they are most common and from which they radiate becoming less and less common towards the periphery. These microspecies are usually closely related to others which have a somewhat wider distribution, and Samuelsson considers the former as derived from the latter.

I think his supposition is right, and starting from this idea I tried to get new forms in my cultures by making them as extensive as possible. I thought that there would be a chance that between a large number of uniform individuals single diverging individuals might appear. This is the same method as that used by H. de Vries in his first *Oenothera Lamarckiana* experiments.

Therefore I sowed as many seeds as possible of several rather widely distributed forms which were tried before by culture after agamization¹.

Each form was constant and produced uniform offspring and apogamically. Each of these new cultures came from seeds of one individual and only from agamized heads. In the four first experiments I got from 100 to 300 plants; the seeds were sown in 1910 and the plants flowered in 1911. In three of the experiments all the plants were uniform and like their parent, but in the fourth experiment, a *H. rigidum* Fr. (*H. tridentatum*) which originally came from a wood near Svendborg, Denmark, I got 154 plants, 153 of which were normal, while one was different in several respects. Some flowerheads of this individual were agamized in 1911, the seeds sown in 1912 and the new generation flowered in 1913. All the plants of this generation were uniform and like their parent, thus different from the original *H. rigidum*. I have later repeated the agamization and sown the seed twice (1912-13 and 1915-16) and obtained the same result.

The new form—I call it *H. rigidum Beta*—was thus at once constant

¹ By the terms "agamization" and "agamize" I mean the process of removing the anthers and the stigmas by means of a cut with a razor before the opening of the flowers of a flower head (the prefix α and the word $\gamma\acute{\alpha}\mu\omicron\varsigma$, marriage).

and produced a uniform offspring. It differs from the original form, *H. rigidum Alpha*, in the following characters (compare the plates):

1. It is lower and smaller in all its parts and the branches are more divaricate.

2. The involucreal leaves (bracts) are more appressed than in *Alpha*, where their tips are more or less recurved; further they are of a lighter colour (fewer dark hairs).

3. Before the flowerhead opens the surface is nearly flat, while in *Alpha* it is distinctly concave, the corollas of the outer unopened flowers reaching higher up than those of the inner ones.

4. In the fully open flowerhead of the *Alpha*-form the corollas of the outermost flowers are much longer than those of the inner ones, while in *Beta* the difference is not so marked and the diameter of the head consequently somewhat less.

I have shortly mentioned (1912, 1919) this result in some papers, but as I had to deal with only one single case I felt it necessary to try to get more material showing the same result. The appearance of the deviating individual might be referable to some experimental error. The probability for such an error was, as far as I could judge, only very slight, as I did not know any form which was like the new one and as all the seeds sown came from agamized heads, but on the other hand one individual was rather unsatisfactory to build upon. Therefore I repeated the whole experiment in an enlarged scale.

In 1915 I agamized a good many heads of a plant of the original *H. rigidum* and of another plant derived from the former after agamization, thus both *Alpha*-individuals. The seeds of each of these two plants were sown in 1916 and flowered in 1917. The offspring of *H. rigidum* itself gave 635 plants like the parent and three "doubtful"; the offspring of the F_1 of *H. rigidum* gave 469 typical plants and one "doubtful." The "doubtful" plants were such as appeared to differ somewhat from the typical, but as the plants stood rather densely, the differences might be caused by conditions. Heads of the four "doubtful" plants and of one typical were agamized, and the seeds were sown in 1918. The new plants flowered in 1920, and it now appeared that the plants from three of the "doubtful" parents did not differ from the typical. But the offspring of the fourth "doubtful" plant (one from the seeds of the original *H. rigidum*) gave 109 plants which were distinctly different from the type, and also different from the first deviating form (*Beta*). We have thus again obtained a deviation which was at once constant, giving uniform offspring.

This new form—*H. rigidum Gamma*—differs from the original *Alpha* in the following characters (compare the plates):

1. It is somewhat lower and with more divaricating branches.
2. The leaves are distinctly broader than in *Alpha*.

On the other hand there is no marked difference with regard to the involucre bracts nor to the shape and size of the flowerheads, only a slight tendency towards the *Beta*-form. The same is the case with the colour of the involucre bracts.

As to the vigour and height the new *Gamma*-form is intermediate between *Alpha* and *Beta*, but it has broader leaves than either of them.

There is a peculiarity which may be of some importance. The original form (*Alpha*) is very fertile after agamization; nearly all achenes are developed and contain sound-looking germs. In *Beta* I have always found many empty achenes and the germinating power is less, while in *Gamma* the fertility is nearer to *Alpha*, although not reaching it.

My experiments show that it is possible to produce new forms apogamically from constant apogamic forms of *Archieracium*, these new forms being themselves apogamic and at once constant. They may be called "*apogamic mutants*." Most probably the numerous microspecies of *Archieracium* found in nature have arisen in that manner.

There seems, to judge from the experiments, to be a contrast between the origin of species in the two subgenera; in *Pilosella* the forms arise by means of hybridization, in *Archieracium* by means of "apogamic mutation." But is this contrast radical?

In *Pilosella* we find species which are partly apogamic and partly sexual as they are able to produce hybrids after fertilization with other species, and at least some of these species are themselves probably—to judge from the polymorphy of the F_1 -generation—to be considered as hybrids. The hybrids produced are apogamic like their parents and owing to apogamy at once constant. If we now cultivate in large numbers such a new form produced by means of hybridization, would it then be possible to get single deviating individuals, as I have shown with regard to *Archieracium*? I have not yet made any thorough experiment, but I should think that we may answer the question in the affirmative. A single experiment which was not completed points in that direction: in a large culture of a race of *H. aurantiacum*—all from seeds obtained after agamization of the heads of a single plant—a single much deviating individual was found, but unfortunately it died before flowering. Supposing that this fact is not due to any experimental error, it speaks in favour of my hypothesis that also within the newly

produced species-hybrids of the *Pilosella* subgenus we may find "apogamic mutants" if we make the cultures extensive enough. And if this supposition is right, it follows that we can declare the "apogamic mutants" as being *after-effects of earlier hybridization*.

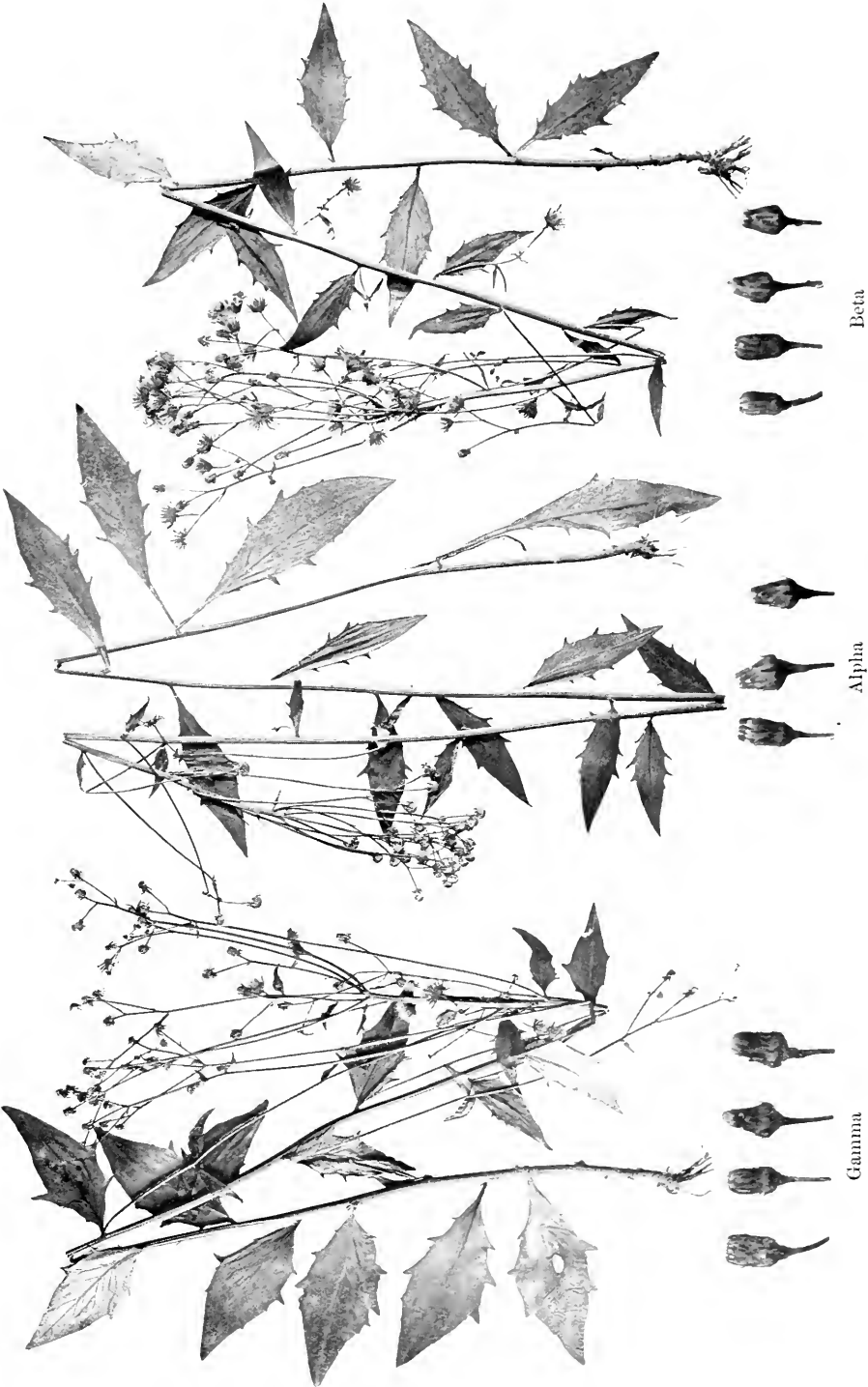
In that way the contrast between *Pilosella* and *Archieracium* disappears. *Archieracium* is then further advanced as regards apogamy, and the microspecies of the present time are either the apogamically seed-setting hybrids from the hybridization-period (as no fertilization takes place we must regard the apogamic propagation as a vegetative propagation, a "klon"-propagation) or "apogamic mutants" arisen from these. In both cases we find a basis of hybridization and *in both subgenera the real cause of the appearance of the many forms is the hybridization, while apogamy is the reason that they keep constant*.

Another question is how this sudden appearance of single "apogamic mutants" as after-effects of hybridization goes on. This is really a cytological problem which I can only touch very briefly. From extensive studies of the cytology of the divisions in the pollen mothercells in many *Archieracium* species Rosenberg (1917) has shown that there are many irregularities. E.g. it happens that single chromosomes do not follow the others in the regular movements during the division; we may, so to speak, say that they are rejected or "forgotten." If we suppose that something similar happens during the division of the embryo-sac mothercell, it would be but natural to think that the "somatic eggcell" in some cases gets a different number of chromosomes, e.g. one chromosome less than ordinarily. The embryo formed without fertilization from such a deviating "somatic eggcell" would produce a plant different from the others derived from the same flowerhead, and in that way we get an explanation of the appearance of the so-called "apogamic mutants." This is of course only a mere hypothesis which has to be proved by cytological investigation, but it is in agreement with the experimental facts.

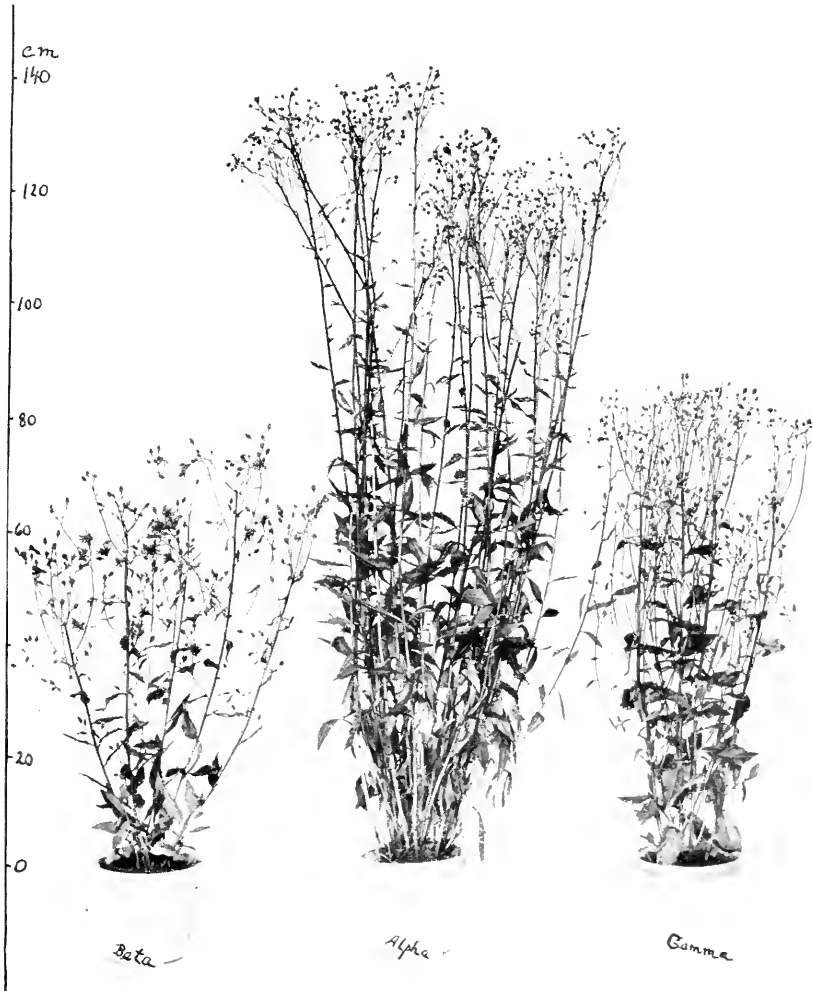
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THE INHERITANCE OF WING-COLOUR IN LEPIDOPTERA.

V. MELANISM IN *ABRAXAS GROSSULARIATA* (VAR. *VARLEYATA*, PORRITT).

By H. ONSLOW.

(With six Text-figures and Plate XIX.)

SEVERAL examples of melanism have already been investigated, and their inheritance described in previous papers. The chief interest of these melanic strains lay in the fact that they were all discovered in the south of England, and far from any manufacturing centres. As appears to be usual, the melanic variety in each case behaved as a simple mendelian dominant.

That exceedingly variable species, *Abraxas grossulariata*, possesses a black variety, known as var. *varleyata*, Porritt¹, found in Huddersfield, and now established as a domesticated strain. Basing his opinion on a single family, bred by Mr L. W. Newman (see the third table), Mr Bateson² concluded that the black variety was not dominant, but recessive to the type form, like the melanic variety of *Odontopera bidentata* (The Scalloped Hazel) investigated by Bowater³. More recently, Porritt⁴ has published the results of some breeding experiments. In 1906 he obtained "a considerable brood," from a mating of *varleyata* \times *varleyata*, all of which proved to be like their parents. Further, in 1907 he obtained a pairing between *varleyata* ♀ \times *grossulariata* ♂ . The latter was a typical wild insect, and 9 ♂ ♂ and 5 ♀ ♀ resulted, all of which were like the male parent. With a view to testing this conclusively, a strain of *varleyata* was procured by the author from Mr L. W. Newman, and both the Rev. G. H. Raynor and Mr Porritt with great kindness furnished some ova.

¹ Porritt, G. T., *Ent. Mo. Mag.* Vol. xli. p. 211, 1905.

² Bateson, W., *Mendel's Principles of Heredity*, 1913, p. 44.

³ Bowater, W. J., *Journal of Genetics*, Vol. iii. p. 299, 1914.

⁴ Porritt, G. T., *Ent. Mo. Mag.* Vol. xliii. p. 12 and p. 276, 1907.

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As it was intended later to carry out experiments with var. *varleyata* and the well-known pale variety, *lacticolor*, some individuals of the latter variety were used in certain pairings, with the result that both *lacticolor* and a completely new variety, with an exceedingly handsome facies, appeared among the F_2 offspring. The genetics of this variety, named var. *exquisita*, Raynor¹, will be dealt with in a future communication. Owing to the occurrence of these varieties, the material in the following tables has been classified into melanic and non-melanic, in order to reduce the number of columns.

The result of mating *varleyata* with non-melanic, that is to say, ordinary wild insects or *lacticolor*, was as follows:

Melanic × *Non-melanic*.

RR × *DD*.

Family	Female	×	Male	Imagines F_1					
				Melanic			Non-melanic		
				Male	Female	Totals	Male	Female	Totals
'16 Z	type	×	<i>varleyata</i>	—	—	—	6	9	15
'18 A	<i>varleyata</i>	×	<i>lacticolor</i>	—	—	—	1	—	1
'18 B	<i>lacticolor</i>	×	<i>varleyata</i>	—	—	—	19	17	36
'18 K	<i>varleyata</i>	×	type	—	—	—	1	—	1
'18 L	„	×	<i>lacticolor</i>	—	—	—	—	3	3
'18 N	„	×	„	—	—	—	1	2	3
'18 O	type	×	<i>varleyata</i> ²	—	—	—	10	10	20
'18 U	„	×	„	—	—	—	8	17	25
'19 K	<i>varleyata</i>	×	<i>lacticolor</i>	—	—	—	3	2	5
'19 W	„	×	„	—	—	—	5	9	14
'19 Z	type	×	<i>varleyata</i>	—	—	—	23	20	43
'19 λ	<i>varleyata</i>	×	<i>lacticolor</i>	—	—	—	2	—	2
'19 μ	„	×	„	—	—	—	5	5	10
Total							178

It is seen that the black variety is recessive both to type and to *lacticolor*. The amount of the black pattern in F_1 individuals appears to vary very considerably, but this point will be dealt with later. Whether *lacticolor* is heterozygous for *varleyata* or not, the variation in the amount of black is usually scarcely noticeable.

¹ Raynor, G. H., *Ent. Rec.* Vol. xxi. No. 11, p. 205, November 1919. It is possible that the variety named *albovarleyata* by Porritt (*Ent. Rec.* Vol. xxix. p. 136, 1917) is *exquisita*, but in answer to some inquiries Mr Porritt says that this form was bred from stock which never contained a single specimen of *lacticolor*; in fact, he had never bred the latter variety. Moreover, although the resemblance is close, there appeared to be some slight but significant difference in the appearance of the black shoulder-knot on the under surface.

² This *varleyata* ♂ was radiated (see p. 136).

The result of mating *varleyata* \times *varleyata* was as follows:

Melanic \times *Melanic*.

RR \times *RR*.

Family	Bred by	Imagines					
		Melanic			Non-melanic		
		Male	Female	Totals	Male	Female	Totals
1906	Mr G. T. Porritt	?	?	28	—	—	—
'18 <i>E</i>	Ova from Mr G. T. Porritt	2	1	3	—	—	—
'18 <i>I</i> *	Ova from Rev. G. H. Raynor	8	5	13	—	1	1
'19 <i>F</i>	H. O.	1	—	1	—	—	—
'19 <i>L</i>	H. O.	5	3	8	—	—	—
'19 <i>O</i>	H. O.	—	1	1	—	—	—
'19 <i>P</i>	H. O.	1	—	1	—	—	—
'20 <i>E</i>	H. O.	9	3	12	—	—	—
'20 <i>G</i>	H. O.	6	3	9	—	—	—
'20 <i>O</i>	H. O.	7	3	10	—	—	—
'20 <i>S</i>	H. O.	8	6	14	—	—	—
'20 <i>W</i>	H. O.	3	2	5	—	—	—
Totals		105	1

* These families contain one or more ♂♂ which are radiated (see table on p. 135).

It is clear that the recessive form breeds true, although the numbers are not large, owing to disease which was particularly severe in 1919. The fact that a single specimen of *grossulariata* appeared in family

*F*₁, *heterozygous* for *varleyata*, inter se.

Family	Bred by	Imagines <i>F</i> ₂					
		Melanic			Non-melanic		
		Male	Female	Totals	Male	Female	Totals
—	Mr L. W. Newman	4	3	7	?	?	24
'17 <i>A</i> *	Ova from Rev. G. H. Raynor	1	1	2	2	1	3
'17 <i>Y</i>	H. O.	2	3	5	5	3	8
1.17	Rev. G. H. Raynor	7	2	9	14	6	20
2.17	"	11	8	19	23	25	48
3.17	"	13	2	15	22	26	48
4.17	"	1	2	3	13	2	15
7.17	"	4	5	9	20	12	32
8.17	"	5	2	7	13	10	23
9.17	"	2	7	9	8	16	24
12.17	"	1	1	2	5	7	12
13.17	"	1	—	1	14	11	25
21.17	"	2	2	4	7	6	13
22.17	"	1	—	1	2	1	3
32.17	"	2	—	2	12	5	17
'18 <i>H</i>	H. O.	—	1	1	—	—	—
'18 <i>T</i> *	H. O.	4	2	6	9	11	20
'19 <i>N</i>	H. O.	1	—	1	—	—	—
'19 <i>V</i> *	H. O.	4	—	4	8	9	17
Totals		107 (23%)	352 (77%)		
Expectation		115	344		

* These families contain one or more ♂♂ which are radiated (see table on p. 135).

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'18 *I* cannot be of any significance, as the ova might very easily have been contaminated before they were received.

By mating together the F_1 heterozygotes, an F_2 generation is produced, which consists approximately of one *varleyata* to three others, either *grossulariata* or *lacticolor*.

I am very much indebted to Mr Raynor for the data of his 1917 families, which are included in the above table. They supplement the other figures, and the totals are fairly close to the expected ratio of 3:1.

All the parents are *grossulariata*, but several of them are dark, and the ♂ parent of 1.17 and the ♀ parent of 22.17 approach var. *hazeleighensis*. Since the parents are in a number of cases heterozygous for *lacticolor*, this variety occurs among the non-melanics in several families.

The result of mating *varleyata* to F_1 heterozygotes shows an almost equal number of melanic and non-melanic, as follows:

		Imagines					
		Melanic			Non-melanic		
Family	Female × Male	Male	Female	Totals	Male	Female	Totals
'18 <i>G</i> *	<i>lacticolor</i> × <i>varleyata</i>	15	13	28	13	14	27
'18 <i>M</i> *	type × <i>varleyata</i>	1	2	3	1	2	3
'18 <i>P</i> *	" × "	12	2	14	12	7	19
'18 <i>R</i> *	<i>varleyata</i> × type	5	8	13	6	8	14
'19 <i>A</i> *	type × <i>varleyata</i>	7	7	14	8	4	12
'19 <i>B</i> *	<i>lacticolor</i> × type	14	10	24	12	8	20
'19 <i>C</i> *	" × "	7	2	9	6	4	10
'19 <i>E</i> *	<i>varleyata</i> × "	9	3	12	5	1	6
'19 <i>G</i>	" × "	2	—	2	1	—	1
'19 <i>H</i>	" × "	—	1	1	2	—	2
'19 <i>J</i>	<i>lacticolor</i> × <i>varleyata</i>	1	1	2	2	1	3
'19 <i>M</i>	<i>varleyata</i> × type	4	4	8	5	3	8
'19 <i>Q</i> *	" × "	8	6	14	12	11	23
'19 <i>R</i>	<i>lacticolor</i> × <i>varleyata</i>	—	1	1	—	—	—
'19 <i>S</i> *	" × "	11	7	18	11	8	19
'19 <i>X</i> *	type × <i>varleyata</i>	4	5	9	2	4	6
'19 <i>Y</i>	<i>varleyata</i> × <i>lacticolor</i>	3	2	5	2	2	4
'19 <i>a</i>	type × <i>varleyata</i>	2	5	7	3	6	9
'19 <i>β</i>	" × "	3	1	4	—	5	5
'19 <i>δ</i>	" × "	—	2	2	1	1	2
'19 <i>ζ</i>	<i>varleyata</i> × type	1	4	5	2	1	3
'19 <i>η</i>	" × "	10	9	19	17	9	26
'19 <i>θ</i>	<i>lacticolor</i> × <i>varleyata</i>	—	1	1	—	—	—
'19 <i>π</i>	" × "	—	2	2	1	3	4
'19 <i>χ</i>	" × "	—	—	—	—	1	1
'19 <i>ρ</i>	type × "	1	—	1	—	2	2
'19 <i>ω</i>	<i>varleyata</i> × type	—	—	—	—	1	1
'20 <i>I</i>	<i>exquisita</i> × <i>lacticolor</i>	6	4	10	2	4	6
'20 <i>J</i>	<i>lacticolor</i> × <i>exquisita</i>	2	1	3	2	2	4
'20 <i>L</i>	type × <i>varleyata</i>	8	1	9	8	1	9
'20 <i>M</i>	<i>exquisita</i> × type	16	9	25	9	6	15
'20 <i>N</i>	<i>varleyata</i> × <i>lacticolor</i>	9	2	11	4	3	7
'20 <i>P</i>	" × "	3	1	4	2	—	2
Totals ...		164	116	280 (51%)	151	122	273 (49%)
Expectation ...				274.5			274.5

* These families contain one or more ♂♂ which are radiated (see table on p. 135).

These figures leave no possible doubt of the recessive behaviour of the melanic variety when mated with *grossulariata*. It will be observed that in both melanics and non-melanics of the last table the ♂♂ are considerably in excess of the ♀♀. These numbers may be compared with those given in the Table on p. 135, where attention is called to this sex ratio.

Var. hazeleighensis, and intermediates.

The normal variety of *varleyata* is shown in Plate XIX. The quantity of white round the base of the wings varies from the amount seen in Fig. 1, where it includes the discoidal spot, to the amount seen in Fig. 10, where practically all the white is gone from the fore wings. It has already been mentioned that the F_1 generation, from *varleyata* × *grossulariata*, often gives individuals which are darker than the normal type form. Fig. 5 shows a typical *grossulariata*; Figs. 6, 11, 12 are forms with increasing amounts of black pigment. The blackest individual, Fig. 12, corresponds to var. *hazeleighensis*, and has fore wings all black, or with a few flecks of white. It will be noticed that its hind wings are not very different from those of the type insect Fig. 5, although the fore wings have actually more black than some examples of *varleyata*.

In order to gain an idea of the amount of black that was present in the intermediate varieties, an attempt was made to measure the extent of the black areas in the different individuals, and to express this as a percentage of the total area of the wing. The following procedure was found to give very satisfactory results. The insects are pinned to a board in such a position that when viewed through a camera lucida¹, a magnification of two diameters is obtained. A drawing is then made of the outline of the wing and of the black pattern. An accurate measurement of the different areas can then be made by means of a planimeter, the maximum error of which is not more than 1 per cent.

This method could with advantage be extended so as to apply to other cases, where the genetics of pattern factors are being studied, such as many problems in the inheritance of coat colour, involving more or less elaborate patterns upon white or coloured grounds. This might be done at least in all cases where the skin could be spread out flat, and would surely be preferable to assigning the specimens to arbitrary grades by means of the eye.

¹ A suitable instrument is sold by Lechertier Barbe, 95 Jermyn Street, S.W. A set of lenses is supplied with the instrument, which are said to enable the operator to make enlargements or reductions to any desired size.

In measuring the black pattern of *grossulariata*, only the fore wings were considered, since the variation in the hind wings is very slight, as may be seen in the plate. Moreover, only a single wing was measured, since the labour involved is very considerable, and the variation between the two wings of the same insect is usually insignificant. In each case, the sum of the black areas on one fore wing was expressed as a percentage of the total area of that wing; the values so obtained were then plotted as distributions¹. It at once became evident that there was a factor, *L*, localising the black pigment to the normal *grossulariata* pattern of the wings. The effect of *l* is to allow the pigment to spread, until the fore wings are as black as in var. *hazeleighensis*. This localising factor *L* was not always carried by *varleyata*, the factor *l* being often introduced by matings with certain dark strains. On account of the increased prices they command, such dark strains are prized by dealers, who would probably pair any *varleyata* to dark rather than to the ordinary type individuals, in the belief that they would be more likely to produce *varleyata* in the next generation. It may here be recalled that the factor causing the black rings round the body of var. *nigrocincta*², though apparently sometimes associated with var. *hazeleighensis*, has been shown to be, like the factor *l*, unconnected with the black variety *varleyata*.

Thus many of the F_1 families coming from strains of *varleyata* obtained from Messrs Newman and Porritt show an increased development of black pigment, which is not apparent in the F_1 families obtained from Mr Raynor's strain. Moreover it has been observed that in addition to this factor *l*, femaleness, or some factor associated with it, prevents the black pigment in the wings of the females from spreading to the extent that it does in the males. A rather similar case has already been described in var. *lutea*³ in which the intensity of the yellow pigment is considerably lower in the females than in the males.

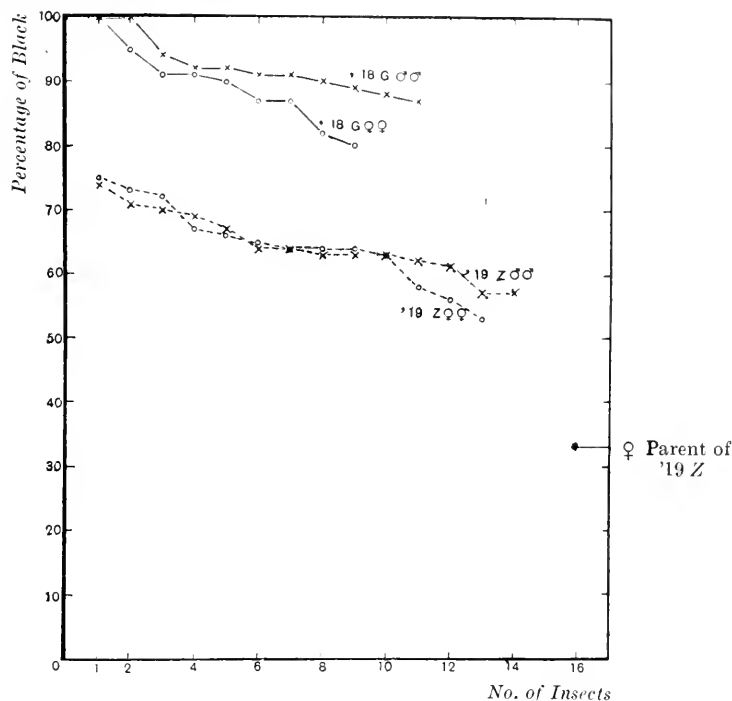
Reference to Text-fig. 1 shows family '19 Z, the F_1 generation from a *grossulariata* ♀ (33 per cent. black) × *varleyata* ♂. It can be seen from the two curves plotted for a certain number of the ♂♂ and ♀♀, purposely selected at random, that the extent of the black pattern is practically the same in both sexes. The average amount of the black pattern was found to be about 64 per cent. of the total area of the fore

¹ The method adopted for making these distributions, as well as the percentage frequency distributions, was exactly the same as that described by Onslow, H., *Journal of Genetics*, Vol. viii. No. 4, p. 209, September 1919.

² Onslow, H., *loc. cit.*

³ Onslow, H., *loc. cit.*

wings. This is more black than is usually found in most type insects, but it is considerably less than that shown in Text-figs. 4 and 6 (about 80 %), which are constructed from insects clearly belonging to dark strains. It is of course probable that there is more than one factor, which by modifying the pattern produce a whole series of insects, in which the area of black varies greatly.

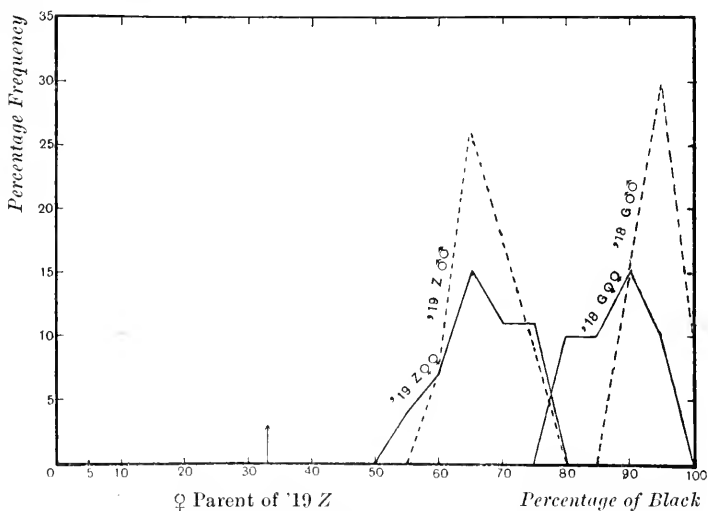


Text-fig. 1 (cf. Text-fig. 2). Curves showing the distribution of the values of the black pattern in F_1 ♂♂ and ♀♀ from the cross *grossulariata* ♀ × *varleyata* ♂ ('19 Z), which appear to carry *L*, the factor localising the black pigment. Similar curves are shown for the black values of *varleyata* in a cross (F_1) ♀ × *varleyata* ♂ ('18 G).

The above points are best seen in the frequency distribution diagram (Text-fig. 2). The curves for both the ♂♂ and the ♀♀ of family '19 Z are similar. They have their maxima at the same point, and they include much the same area.

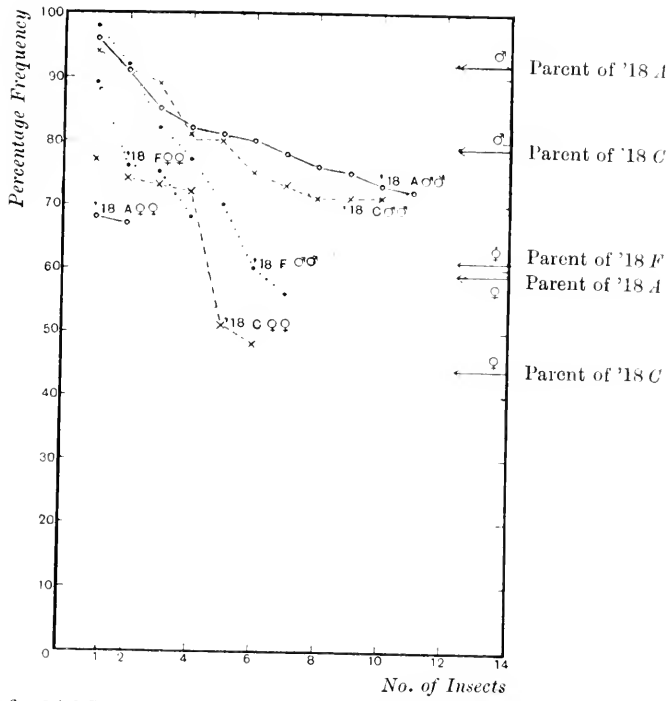
In the diagrams showing the frequency distributions the percentage of the black area is given along the base line, and the percentage frequency of any given black value is shown on the left-hand side. Thus,

the maximum of the curve denotes that percentage of black which occurs most frequently. In the case of the curves showing the distributions of the black values, the figures along the base line denote the number of individuals. Each individual is represented by a cross, a circle or some other sign, which is the same for both sexes of any given family. The percentage of black in the pattern is shown on the perpendicular at the left-hand side. The name of the family and the sex are written against each curve, whereas the percentage of black in the *grossulariata* pattern of each parent is shown by an arrow at the correct point on the right-hand side.

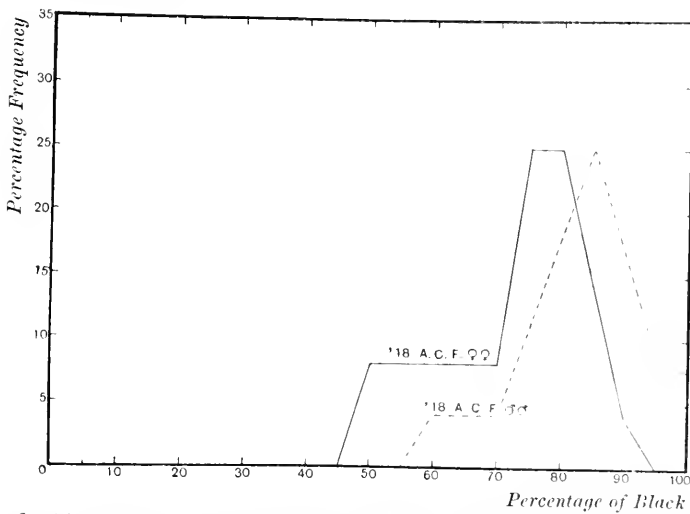


Text-fig. 2 (cf. Text-fig. 1). Diagrams showing the frequency distribution of the values for the black pattern in the ♂♂ and ♀♀ of the families shown in Text-fig. 1.

Text-fig. 3 shows a group of families from a dark strain of Mr Newman's, which carries the factor, *l*, leading to an increase of the black pattern, but not the factor for *varleyata*, thus showing conclusively the independence of these two factors. The appearance of these curves is very different from that of '19 Z (Text-fig. 1), and the salient points are best seen in the frequency distribution, Text-fig. 4, in which the males and females of all three families are combined in two curves. The average extent of the black pattern is obviously greater than in type strains, and this increase of black is greatest in the curve for the males, as may be seen from the fact that its maximum falls to the right of that of the ♀♀ curve. The average value for the black pattern, when both ♂♂ and ♀♀ are considered, is about 80 per cent.; that of the ♀♀ about 78 per cent., and that



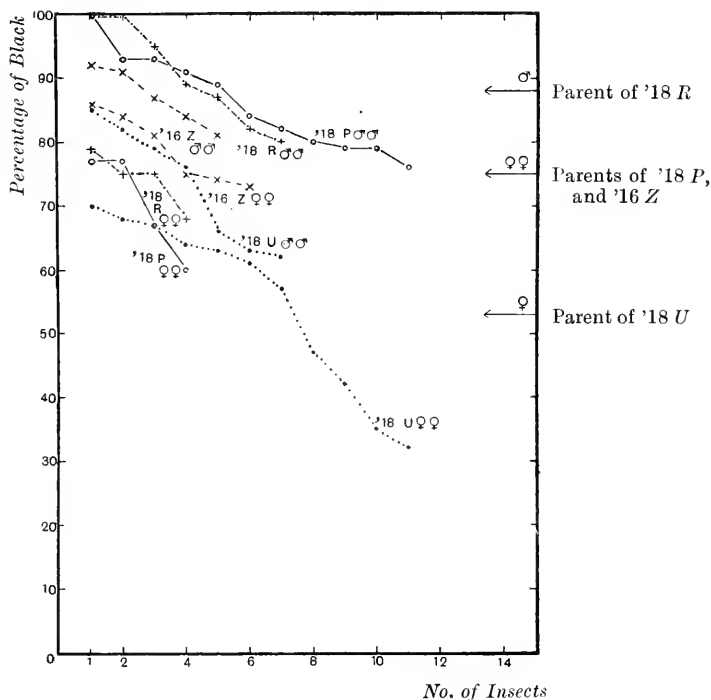
Text-fig. 3 (cf. Text-fig. 4). Curves showing the distribution of the values of the black pattern in ♂♂ and ♀♀ from three families of *grossulariata* × *grossulariata* ('18 A, C, F). They carry the factor, *l*, leading to an increase of the black pattern which affects ♂♂ more than ♀♀, but not the factor for *varleyata*.



Text-fig. 4 (cf. Text-fig. 3). Diagram showing the frequency distribution of the values for the black pattern of the ♂♂ and the ♀♀ in the three families of Text-fig. 3.

of the ♂♂ about 85 per cent. If the families are considered separately, the darkest parents, as might be expected, appear to have the blackest offspring. This may be seen by a glance at the values for each parent, shown by the arrows on the right-hand side, where families '18 A and '18 C (Text-fig. 3) seem to have the darkest parents. The ♂ parent of '18 F was unfortunately lost, but a note remains describing it as rather darker than type, and probably with a black value of about 60 per cent.

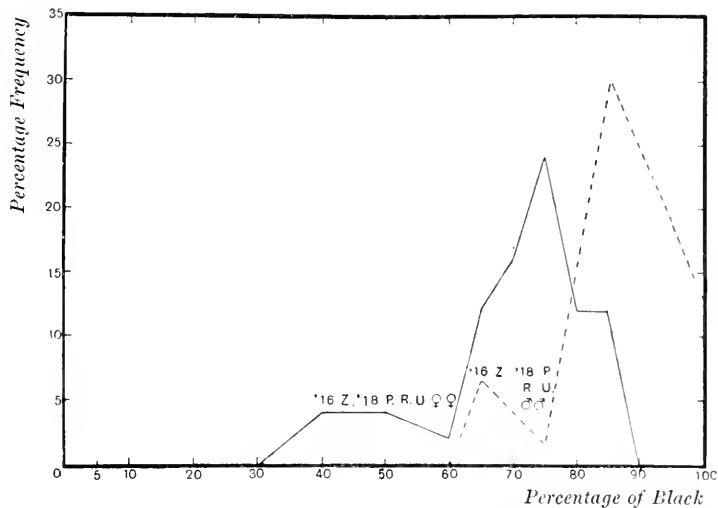
The curves shown in Text-fig. 5 represent families which carry both the factor, *l*, leading to an increase of the black pattern, and the factor for



Text-fig. 5 (cf. Text-fig. 6). Curves showing the distribution of the values for the black pattern in F_1 ♂♂ and ♀♀, from the cross *grossulariata* ♀ × *varleyata* ♂ ('16 Z and '18 U). Similar distributions are given for *grossulariata* ♂♂ and ♀♀ from the cross F_1 × *varleyata* ('18 P and '18 R). The effect of the factor *l*, which leads to an increase of the black pigment, can be seen in both sexes, but more so in the ♂♂ than in the ♀♀.

varleyata. Families '16 Z and '18 U are the F_1 generation from the cross *grossulariata* ♀ × *varleyata* ♂, and their average black value is greater than in type specimens, and also greater in the ♂♂ than in the ♀♀. The two other families in the same figure, '18 P and '18 R, are *grossulariata*

from the cross (F_1) \times *varleyata*, and they illustrate practically the same points as the previous insects. This is best seen in the frequency distribution diagram (Text-fig. 6) in which the ♂♂ and ♀♀ of all four families have been combined in two curves. The average black value is about 80 per cent., that of the ♀♀ being 75 per cent. and that of the ♂♂ 85 per cent., that is to say, the percentage of black on the fore wings is (1) greater than in the type specimens, and (2) greater in the ♂♂ than in the ♀♀.



Text-fig. 6 (cf. Text-fig. 5). Diagram showing the frequency distribution of the values for the black pattern of ♂♂ and ♀♀ in the four families in Text-fig. 5, combined together.

As might be expected, it makes no apparent difference which parent is the *varleyata*; for instance, family '18 R comes from a *varleyata* ♀ \times *grossulariata* ♂ (88 per cent. black), and family '18 P comes from a *grossulariata* ♀ (75 per cent. black) \times *varleyata* ♂ (see Text-fig. 5). The correlation between the black values of the parents and the offspring is also clearly seen. The arrows on the right-hand side of Text-fig. 5 show the parental values, which in the case of '18 U is 57 per cent. The offspring of this mating are not so dark as the other two families, the parental values of which are 75 and 88 per cent. Readings were made from only a small number of families, owing to the great labour involved, but the curves given are representative of all the families in the preceding tables, in which the two classes—those which inherit the localising factor *L*, and those which do not—can be very clearly differentiated.

A consideration of families 1.17 and 22.17 (*hazeleighensis* \times *grossulariata*) seems to show that the factor *l* is probably recessive when crossed with the type form, but the fact that there may be more than one modifying factor, no doubt, complicates the case considerably.

It has already been mentioned that there is a considerable variation in the size of the white collar of *varleyata* (see Plate XIX, figs. 1—4 and 7—10). Not improbably, this variation has been introduced from the dark strain of *grossulariata*, either by or in association with the factor *l*. However, the variation is not found to be most highly developed in those families which show the greatest increase of the black pattern. If the restriction of the white collar of *varleyata* were clearly associated with an extension of the black pattern of *grossulariata*, it would undoubtedly behave in the same way. Measurements were made of certain *varleyata* ♂♂ and ♀♀ of family '18 G from a cross, F_1 ♀ \times *varleyata* ♂. Text-fig. 1 shows the percentage of black on the fore wings of these *varleyata*. This varies between 80 and 100 per cent., and moreover there is a small difference between the black values of the ♂♂ and ♀♀, amounting to about 4 per cent. in favour of the ♂♂, a value which should be above the experimental error, though not of much significance.

The relationship of the curves for the two sexes may best be seen by reference to Text-fig. 2. It seems possible that even if there were an inhibiting factor associated with femaleness, its effect might be very difficult to measure, on account of the small area of white present in the variety. It was accordingly considered not worth while to undertake a more extensive series of measurements.

Vars. actinota and leucosticta.

Another interesting variety of *varleyata*, which appeared during the experiments, was that showing a varying amount of radiation (Plate XIX, figs. 7, 8 and 9). This variety, which shows a white radiation upon a black ground, must not be confused with var. *radiata*¹, in which the radiation consists of a prolongation of the black marginal spots. The amount of radiation varies from a mere fleck of white on the hind wings, as in Plate XIX, fig. 7, to the striking wedge-shaped markings of fig. 9, which can be seen to extend even to the fore wings. For the first form Mr Raynor has suggested the name var. *leucosticta*, and for the fully radiated form var. *actinota*. This character behaves quite independently of the factor *L* which leads to a restriction of the black pigment.

¹ Onslow, H., *Journal of Genetics*, Vol. VIII. No. 4 (see p. 221, and Plate IX, fig. 56).

In the preceding tables the families in which these radiated individuals occur have been indicated by an asterisk. The number of radiated individuals in these families is now given in the following table:

Families containing the radiated varieties actinota and leucosticta.

Family	Female × Male	Imagines							
		Radiated	Melanic			Non-Melanic			
			Male	Non-radiated		Totals	Male	Female	Totals
				Male	Female				
'18 I	<i>varleyata</i> × <i>varleyata</i>	1	7	5	13	—	1	1	
'17 A	type × type	1 (I)	—	1	2	2	1	3	
'18 T	„ × „	1	3	2	6	9	11	20	
'19 V	„ × „	4 (I)	—	—	4	8	9	17	
'18 G	<i>lacticolor</i> × <i>varleyata</i>	1	14	13	28	13	14	27	
'18 M	type × „	1	—	2	3	1	2	3	
'18 P	„ × „	7 (3)	5	2	14	12	7	19	
'18 R	<i>varleyata</i> × type	3	2	8	13	6	8	14	
'19 A	type × <i>varleyata</i>	2	5	7	14	8	4	12	
'19 B	<i>lacticolor</i> × „	3 (I)	11	10	24	12	8	20	
'19 C	„ × „	2	5	2	9	6	4	10	
'19 E	<i>varleyata</i> × type	9 (9)	—	3	12	5	1	6	
'19 Q	„ × „	5	3	6	14	12	11	23	
'19 S	<i>lacticolor</i> × <i>varleyata</i>	1 (I)	10	7	18	11	8	19	
'19 X	type × „	2	2	5	9	2	4	6	
Totals ...		43 (16)	67	73	183	107	93	200	

The broods come from three different types of mating. The figures in brackets against the radiated specimens denote the number of those heavily radiated (var. *actinota*), the remainder are all var. *leucosticta*. The most interesting fact to be noted is that all 43 radiated insects are ♂♂, not a single ♀ showing any trace of this character. The association of this variation with maleness seems to be complete, for I am informed by Mr Raynor that he has bred 104 specimens of var. *actinota* in 1920, and almost as many of var. *leucosticta*, and they do not include a single female. Moreover, Porritt¹ mentions a similar case (see Family 1906 in the second table, p. 125) in which all the ♂♂ were radiated, but not a single ♀. Recently, however, this observer has bred from radiated stock a *leucosticta* ♀.

The greatest number of radiated individuals is found in family '19 E which has 9 *actinota* ♂♂, but the study of the pedigree of this and the other families gives no clue to the type of inheritance followed. When a radiated insect is mated to *grossulariata* (i.e. family '18 O, see first

¹ Porritt, G. T., *Ent. Mo. Mag.* London, Vol. XLIII, p. 12, 1907.

table, p. 124), the character cannot appear in the type offspring, even if the necessary factors were present, because radiation is essentially a variation of *varleyata*, and could not show on the *grossulariata* pattern.

It would seem as if the white radii ought to be a remnant of the dominant white ground of *grossulariata*, which shows through the black of *varleyata*, and therefore the radiated varieties should be dominant to *varleyata*. Inspection of the last table, however, shows that in family '18 I one radiated insect was bred from two *varleyata* parents, but even if this radiated insect is accounted for, by supposing it to have been introduced accidentally like the single *grossulariata* in the same family, it is seen that the black parents of all the other radiated insects are normal. Supposing radiation to be dominant the *grossulariata* parents would have to be heterozygous for the factor, in which case the ratio between radiated and non-radiated *varleyata* should have been one of equality, whereas it is 43 radiated to 140 non-radiated.

From the scanty data in the last table it is impossible at present to determine the inheritance of this variation with any certainty, but the fact that there is in *Abraxas* a factor linked to maleness, as well as one linked to femaleness (*lucticolor*), is of some interest, for, except in *Drosophila* this has not been recorded. Suppose in the first place it is assumed that the case is as simple as possible, the factor for radiation being sex-linked to the male, and recessive to *varleyata*. Then if both parents are heterozygous for the recessive factor, considering the melanic offspring, which alone can show the radiation, there should be one radiated male, one normal male and two normal females, or 45.75 radiated to 137.25 non-radiated. This does not differ much from the ratio actually found, which was 43 radiated to 140 non-radiated. The suggestion, however, takes no account of a very important point in connection with the ratio of the sexes, to which attention has not as yet been drawn.

Among the type insects the sexes approach equality, but among the melanics there are 110 ♂♂ to 73 ♀♀. This looks as if there is a missing group of ♀♀ which correspond to the radiated ♂♂, a fact suggesting the operation of a lethal factor. It is curious, however, that the missing ♀♀ should be restricted to the melanics, and it looks as if the lethal factor is only effective when a female is both radiated and melanic. If this were so, the ratio of the sexes would be much closer to the figures actually obtained, but on the other hand the number of radiated ♂♂ should be only 26, instead of 43 as recorded.

In trying to account for this unusual sex ratio, if only the factor for radiation were in spite of the evidence found to be dominant, an analogy

suggests itself with the inheritance of "notch" wing in *Drosophila*¹. This variation is dominant and sex-linked to the female; associated with the homozygous condition is a lethal factor, causing homozygous females to die, but the heterozygous females live. Moreover, all males carrying "notch" die, because the *Y* chromosome is supposed to be empty, and therefore the insects do not possess the normal allelomorph for "notch" which, in the heterozygous females, counteracts the lethal factor. If in the case of radiation, conditions were the same, except that the factor was linked to the male sex, then *varleyata* ♀♀ (het. for radiation) × *varleyata* ♂♂ should give equal numbers of *varleyata* ♂♂ and ♀♀, and the same number of radiated ♂♂, but no radiated ♀♀.

When more data are available, it will be easier to decide whether a lethal factor is present or not; also whether "notch" wing, colour-blindness, or some other mode of inheritance is the most correct type on which to base the explanation of the anomalous sex-ratio observed. At present only some of the possibilities can be indicated, but it should be remembered that, whatever explanation is adopted, it must take into account the fact that at least one radiated female has been produced. Moreover, attention may be called to the sex ratio in the *varleyata* × *F*₁ families (see p. 126) which show a considerable excess of males in both black and type insects, no matter whether the radiated families, marked with an asterisk, are included or not.

If the factor for radiation is supposed to be recessive, and sex-linked to the male, Professor Punnett has raised an interesting question. Supposing the missing chromosome observed by Doncaster in the all-female strains of *grossulariata* to be a sex chromosome, then according to the chromosome hypothesis, the factor for radiation would be carried by the *Z* chromosome. A female, heterozygous for radiation, would have that factor in her *Z* chromosome. Thus if Morgan's suggestion that the *W* chromosome is a "dummy" without factors, is accepted, then all such heterozygous females must be radiated in appearance. To avoid this difficulty, either the *W* chromosome must carry the normal allelomorph which prevents the development of the white radiation, or the *W* chromosome itself must be able to inhibit radiation in a female that is genetically *actinota*, which is after all much the same thing. From his work on poultry, Professor Punnett² is inclined to believe that if sex chromosomes exist in these cases, they can carry factors.

¹ Morgan, T. H., *Publications of the Carnegie Institute*, No. 343, 1919.

² Punnett, R. C., *Journal of Genetics*, Vol. xi. No. 1, p. 37, April, 1921.

CONCLUSIONS.

1. In *Abraaxas grossulariata* the factor for the black pattern of var. *varleyata* behaves as a simple mendelian recessive both to the type form and to var. *lacticolor*. A new variety, *exquisita*, which probably contains both recessive factors, that for *varleyata* and that for *lacticolor*, will be dealt with in a subsequent communication.

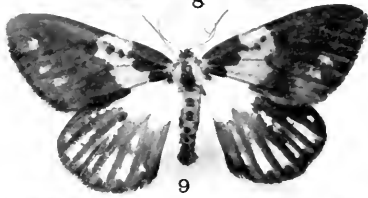
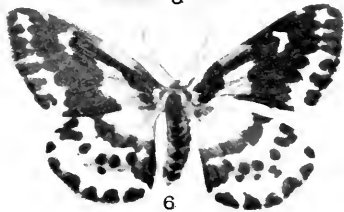
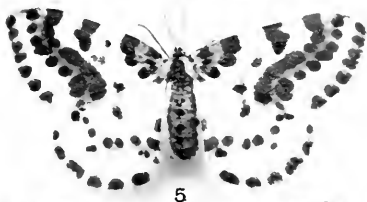
2. The type *grossulariata* carries a factor *L*, which localises the black pigment to the normal pattern. The factor *l* allows the black pigment to spread until it almost covers the fore wings as in var. *hazeleighensis*. This variation appears to behave as a recessive when mated to type insects. It is inherited independently of the factor for *varleyata*, but is often introduced by crossing this variety with dark strains of *grossulariata*.

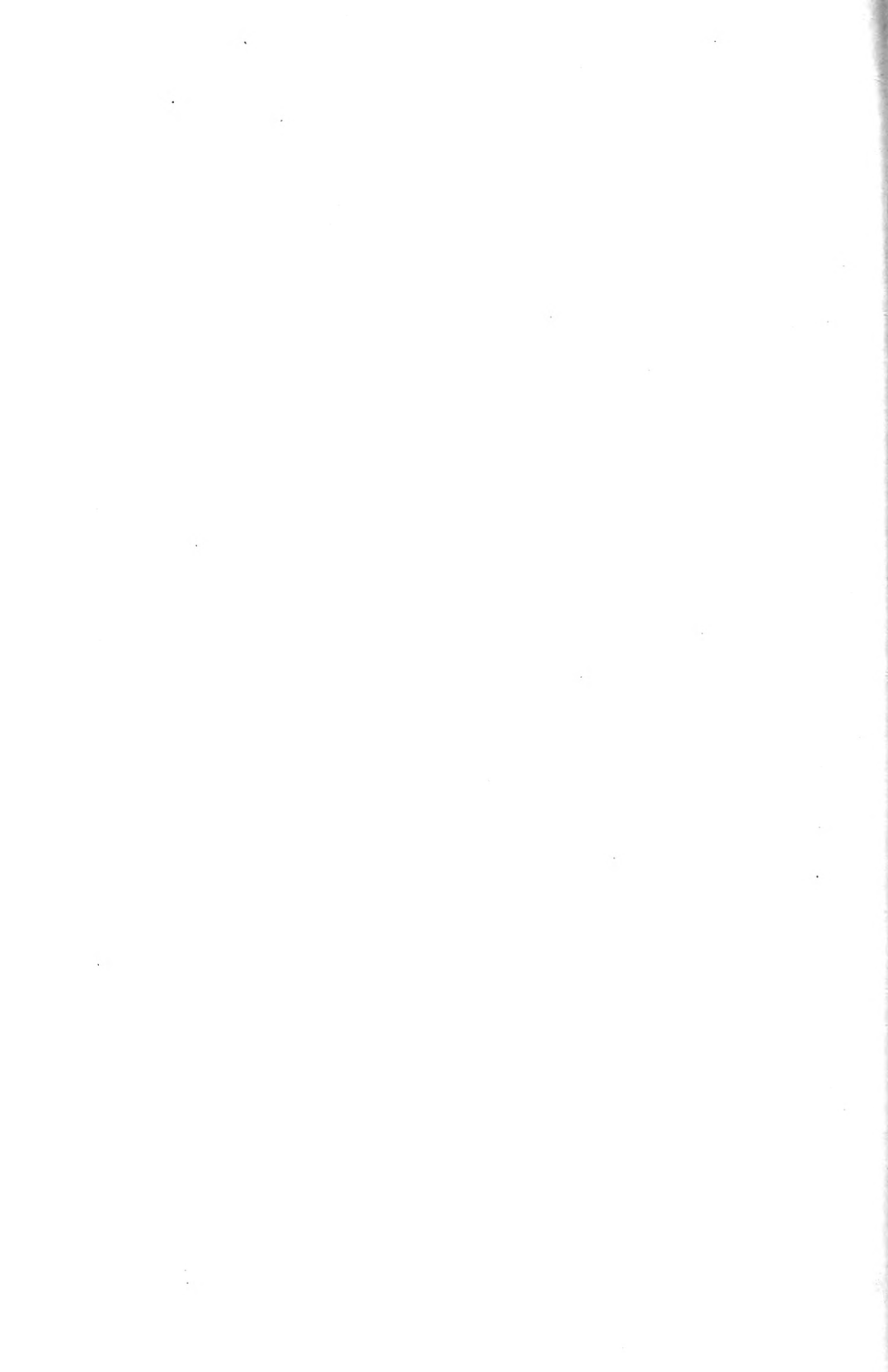
3. A method is described by which the black pattern can be measured, and its area expressed as a percentage of the total extent of the fore wings. The values of the black pattern in several families were obtained, and were plotted as distributions and as percentage frequency distributions.

4. These diagrams show that in certain families the amount of black in both sexes is considerably greater than in the type form, and that the darkest parents have as a rule darker offspring than lighter parents. Moreover, the percentage of black in the ♂♂ is considerably greater than in the ♀♀, suggesting that femaleness or some factor associated with it prevents the full development of the pigment.

5. The size of the white collar in var. *varleyata* varies considerably. This is possibly in some way connected with the factor *l*, for measurements of one family show that the ♀♀ have slightly less white than the ♂♂, but the amount can scarcely be considered significant.

6. A variety showing a fluctuating amount of white radiation on the black ground of *varleyata* has been found, which appears to be linked to the male in a manner analogous to that in which *lacticolor* is linked to the female. At first sight it appears that this white radiation should be part of the dominant white ground of *grossulariata*. Nevertheless, there seems to be some evidence to show that it is recessive to *varleyata*. Since this radiation is a modification of the black ground, it is clear that it cannot show in *grossulariata* insects, even if they carried the factors necessary to produce it. The ratio of one radiated ♂ to





three non-radiated ♂♂ and ♀♀, which would result from the hypothesis that radiation is recessive, and that both parents were heterozygous, is closely approached by the actual figures. It is, however, an hypothesis that takes no heed of the remarkable sex ratio which shows a large preponderance of males.

There are not at present enough data to determine whether this disturbance of the normal sex ratio can be explained better by the action of a lethal factor or not, but the work is being continued.

In conclusion my thanks are due to the British Association for defraying part of the expenses of this research by a grant during the year 1920. I am also much obliged to the Rev. G. H. Raynor both for the data and for the living material he has so kindly allowed me to use, and to the editors for their kindness in reading this paper. I am especially grateful to Miss Helen Moodie for her care of the larvæ, and the resulting large families.

DESCRIPTION OF PLATE XIX.

Abraxas grossulariata and varieties. Natural size.

1. Var. *varleyata* ♀ with broad white collar showing discoidal spots.
2. Var. *varleyata* ♀ with black stripe crossing collar from basal shoulder knot to discoidal spot.
3. Var. *varleyata* ♀ with narrow collar showing spread of black pigment outwards from basal shoulder knot.
4. Var. *varleyata* ♀ except for a white fleck the collar is restricted to the hind wings.
5. *Grossulariata* ♀, type, showing normal pattern.
6. *Grossulariata* ♀ showing increase of black pigment, also stripe as in No. 2.
7. Var. *leucosticta* ♂, a black insect showing traces of two white radii near margin of hind wings.
8. Var. *leucosticta* ♂ showing number of incomplete radii on hind wings.
9. Var. *actinota* ♂ showing fully radiated hind wings with traces of radiation on fore wings.
10. Var. *varleyata* ♂ showing, like No. 4, almost complete absence of white collar on fore wings.
11. Var. *hazeleighensis* ♂ showing considerable increase of black pigment, though the white areas are rather too extensive for this variety.
12. Var. *hazeleighensis* ♂ showing black pigment almost entirely covering the fore wings.

Note. Those insects whose fore wings show a great increase of black pigment have little or no corresponding increase in the hind wings.

SEX-REVERSAL IN FROGS AND TOADS. A REVIEW OF THE RECORDED CASES OF ABNORMALITY OF THE REPRODUCTIVE SYSTEM AND AN ACCOUNT OF A BREEDING EXPERIMENT.

By F. A. E. CREW.

*(Papers from the Animal Breeding Research Department,
The University, Edinburgh.)*

(With Twenty-three Text-figures.)

THE abnormalities which have been recorded can be so tabulated that the first case most nearly approximates to the normal female and the last the typical male, with respect to the nature of both primary and secondary sexual characters. Thus arranged, it is seen that the cases furnish an almost complete series of gradations which range from an individual almost completely female, to one almost completely male, and that the conditions found readily appear to be merely graded stages of a single process.

A. RANA.

DIVISION I. THOSE CASES IN WHICH THE SECONDARY SEXUAL CHARACTERS WERE NOT TYPICALLY MALE.

Group A. Those cases in which, on inspection, one gonad was an ovary and the other an ovo-testis.

Sub-group 1. The ovary was normal in appearance.

1. BOURNE. *R. temporaria*. Adult. Secondary sexual characters were not described.

Right gonad. An ovary.

Left gonad. An ovo-testis. The larger ovary-portion bore along the anterior half of its inner border the smaller testis portion.

Vasa efferentia could not be observed.

Seminal vesicles not present.

Müllerian ducts well-developed.

On section. Ovary-portion of the ovo-testis contained well-developed ova; testis portion contained motile spermatozoa; and there was no distinct line of separation between ovary- and testis-portions.

2. YOUNGMAN. *R. temporaria*. Adult. Killed June. Secondary sexual characters male but poorly developed.

Right gonad. An ovo-testis. An ovoid non-pigmented testis-portion suspended from the ventral surface of a small but apparently normal ovary.

Left gonad. An ovary of normal appearance.

Vasa efferentia. "There appears no means of exit to the exterior for the spermatozoa, unless they burst into the coelom, for I can make out neither macroscopically nor microscopically by sections, any trace of vasa efferentia, and sections of the ureter do not show the presence of spermatozoa therein."

Seminal vesicles not present.

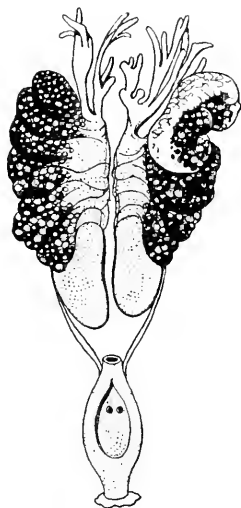


Fig. 1.



Fig. 2.

Müllerian ducts exceedingly well-developed with eggs within the convoluted portions of each and with uterine segments crammed to distension.

On section. Left ovary and the dorsal ovary portion of the right gonad showed the following structure. Numerous normal ova were present, but there were also cavities among the ordinary egg-containing chambers, and of the same size, which were filled with black pigment ("representing perhaps degenerate eggs"). The ventral testis-portion of the ovo-testis showed testicular structure, and contained immature and mature spermatozoa and, in addition, peculiar eosinophilous bodies.

Sub-group 2. The ovary was abnormal in appearance.

3. HUXLEY. (1.) *R. temporaria*. Adult. Killed April. Secondary sexual characters as those of a well-developed female. No male characters were present.

Right gonad. An ovary of usual size but more deeply pigmented than usual.

Left gonad. An ovo-testis consisting of an ovary of unexceptional size, which bore upon its ventral surface a small nodule of testis material.

Vasa efferentia were not present in connection with the right gonad but there were two in association with the testis-portion of the ovo-testis.

Seminal vesicles were present, being very small and spindle-shaped.

Müllerian ducts were well-developed and ova were contained therein.

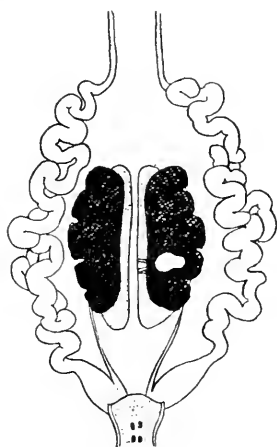


Fig. 3.

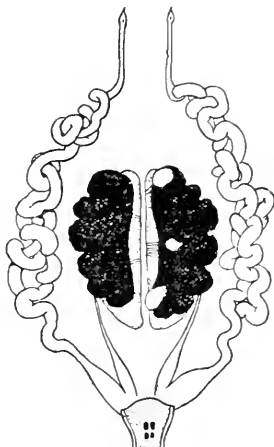


Fig. 4.

On section, the right gonad was seen to be entirely ovarian in structure, the fibrous tissue of the ovarian wall was everywhere hyperplastic and there was excess of pigment.

The left gonad consisted of two portions. The smaller was composed of spermatid and the larger of ovarian tissue similar in structure to the ovary of the opposite side. The spermatid tissues were healthily normal for the most part, but ova were found amid them, within and between the seminal tubules. An ovum within a tubule lay among spermatozoa which were deformed and degenerate, a consequence possibly of the pressure exerted by the ovum. The seminal tubules in the neighbourhood of an ovum which lay between the seminal tubules were contorted and

misshapen and the intertubular connective-tissue in this area was hyperplastic.

There was ciliated epithelium upon the peritoneum, and the ova within the Müllerian ducts were all degenerate.

4. CREW. (J.) *R. temporaria*. Adult. Killed April. Secondary sexual characters male but imperfectly developed.

Right gonad. An ovary, somewhat firmer and more strongly pigmented than usual.

Left gonad. An ovo-testis, having the appearance of an ovary rather more deeply pigmented and firmer to the touch than usual, which bore along its inner border three small nodules of testis-substance.

Vasa efferentia—few in number—were present on either side.

Seminal vesicles were present, being small and fusiform.

Müllerian ducts very well-developed, ova within uterine segments and convoluted portions.

On section. Right ovary and ovary-portion of the left gonad entirely ovarian in structure, but practically all of the more mature ova showed signs of degenerative changes. There was widespread increase of the pigment normally present in an ovary and the connective-tissue was distinctly hyperplastic. The three nodules upon the inner border of the left gonad had the structure of normal spermatatic tissue.

There were ciliated cells upon the peritoneum. The Müllerian ducts contained only degenerate and spurious ova.

5. MARSHALL. (D.) *R. temporaria*. Adult. Secondary sexual characters not described.

Right gonad. An ovo-testis. The larger testis-portion had the ovarian tissue disposed along its outer border. The body of the testis-portion presented upon its ventral surface a very deep transverse groove. At the anterior end of the ovary-portion was a deeply pigmented lobule which was bent back over the dorsal surface of the gonad.

Left gonad. An ovary more strongly pigmented than usual and divided into six lobes by well-marked constrictions.

Vasa efferentia on the right side as those of the normal male; two or three thin-walled tubules connected the left ovary to its kidney.

Seminal vesicles not present.

Müllerian ducts well-developed.

On section, the greater part of the right gonad had the structure of normal testis. The pigmented band, which ran along its outer border, extended inwards about a quarter of the way through the substance of the testis, and consisted of masses of pigment which followed the lines

of the intertubular connective tissue, this being hyperplastic in these areas. The polygonal masses of pigment were, in most cases, entirely outside the seminal tubules which had become crushed together and obliterated by the increase of the intertubular connective-tissue, and only in the last stages of atrophy of the tubules were pigment found within them. The dorsal lobe of the ovo-testis and the left gonad showed exactly similar structure, that of ovary with hyperplastic connective tissue and great abundance of pigment. Few ova were found which were in a thoroughly healthy condition and the great majority were in various stages of degeneration, the protoplasm having shrunk from the follicle wall, the nuclei being of small size, and the follicle in some cases invaded by pigment.

"It is worthy of note that while the male portion of the essential glands is absolutely normal throughout, the female portion, though more bulky, forming the whole of the left gland and part of the right one as well, is not normal in any part, the majority of the ova showing more or less well-marked signs of degeneration, and the whole structure exhibiting very obvious sclerotic induration, which must be regarded as pathological."

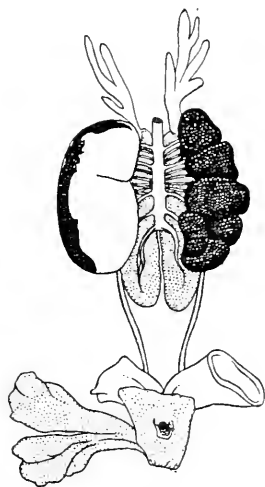


Fig. 5.



Fig. 6.

Group B. Those cases in which, on inspection, both gonads were ootestes.

6. HOOKER. (B.) *R. fusca*. Adult. Killed October. Secondary sexual characters imperfectly developed male, but in addition the skin of the back was warty.

Right gonad. An ovo-testis. To the outer border of the larger testis-portion the smaller ovary-portion was attached.

Left gonad. An ovo-testis, having the form of a normal-sized six-lobed ovary which had a small nodule of spermatie tissue attached to the middle of its inner border.

Vasa efferentia of the usual male pattern.

Seminal vesicles present, being small and spindle-shaped.

Müllerian ducts well-developed.

On section of the left gonad (it was assumed that the right was similar), the testis-portion, discrete from the ovary-portion, showed the structure of normal testis; the ovary-portion contained large numbers of ova, some immature, some mature, and many showing various stages of degeneration, being associated with black pigment.

7. SMITH. *R. temporaria*. Adult. Secondary sexual characters male but imperfectly developed. (The skin below the throat was lighter on the left side; the typically male pad was present on the index finger of the right side only.)

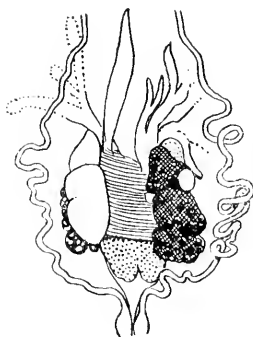


Fig. 7.

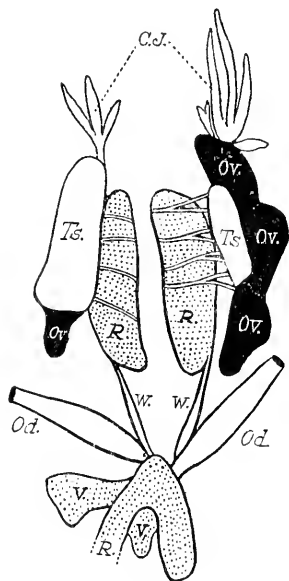


Fig. 8.

Right gonad. An ovo-testis. The larger testis-portion presented several constrictions upon its surface and bore along the outer border the smaller ovary-portion, on the surface of which the outlines of ova could be distinguished.

Left gonad. An ovo-testis consisting of a larger ovary-portion bearing upon its inner border a nodule of spermiatic tissue. There was a second nodule of this tissue upon the outer border.

Vasa efferentia (of the usual male pattern?).

Seminal vesicles not present.

Müllerian ducts—right moderately, left well-developed.

No sections made.

Group C. Those cases in which, on inspection, one gonad was an ovo-testis and the other a testis. None.

Group D. Those cases in which, on inspection, both gonads were testes. None.

DIVISION II. THOSE CASES IN WHICH THE SECONDARY SEXUAL CHARACTERS WERE TYPICALLY MALE.

Group A. Those cases in which, on inspection, one gonad was an ovary and the other an ovo-testis. None.

Group B. Those cases in which, on inspection, both gonads were ovotestes.

8. BOULANGÉ. *R. fusca*. Adult. Killed December. Secondary sexual characters typically male.

Right gonad. An ovo-testis of which the testis-portion constituted three-quarters of the whole gonad and was situated anteriorly.

Left gonad. An ovo-testis of which the three-lobed ovary-portion formed four-fifths of the whole and encompassed the testis-portion which lay upon its inner border.

Vasa efferentia were present in association with the testis-portions of both gonads.

Seminal vesicles were not present.

Müllerian ducts well-developed.

On section, the ovarian portions showed the structure of normal immature ovaries: the testis-portions, that of normal testis.

9. PUNNETT. *R. temporaria*. Adult. Killed February. Secondary sexual characters male.

Right gonad. An ovo-testis with a very large testis-portion bearing a deep constriction upon its inner border. The ovary-portion was merely a patch of ovarian tissue situated upon the outer border of the testis-portion exactly opposite the constriction upon the inner border, and it lay within a deep angle of testicular material.

Left gonad. An ovo-testis with a larger six-lobed ovary-portion, upon the inner border of which, at about its mid-point, was situated a small spherical lobule of testicular substance.

Vasa efferentia entered into functional relationship with the spermatie and ovarian tissues of both gonads.

Seminal vesicles small and fusiform.

Müllerian ducts well-developed.

On section, the ovarian patch upon the right gonad contained but a single ovum, and the rest of this gonad was purely testicular. The testicular patch upon the left gonad had the structure of normal testis but at one point it contained a well-developed ovum.

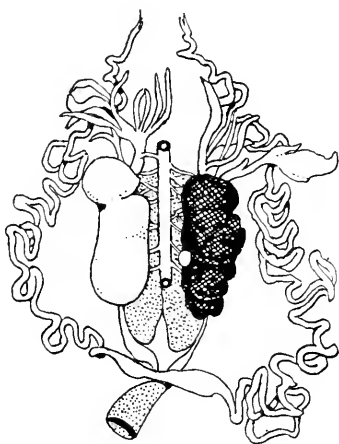


Fig. 9.

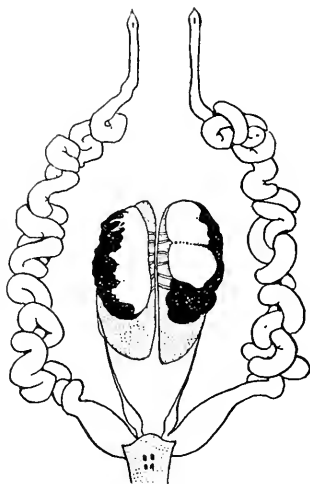


Fig. 10.

10. CREW. (2.) *R. temporaria*. Adult. Killed June. Secondary sexual characters typically male.

Right gonad. An ovo-testis having the appearance of a malformed testis, irregular in outline and with its surfaces scored with deep grooves, which bore along its outer border a broad band of dense black pigment, which in some places was flatly applied to the surface of the testis and in others was piled up into nodular prominences resembling ova.

Left gonad. An ovo-testis consisting of three lobes, of which the anterior and middle were testicular, but bore a band of dense black pigment similar to that of the opposite gonad along the outer border, while the posterior lobule was ovarian, the pigment of which was continuous with the band upon the outer border of the other two.

Vasa efferentia present on both sides.

Seminal vesicles, pigmented and of moderate size were present.

Müllerian ducts were well-developed.

On section, the right gonad consisted of normal spermiatic tissue in all parts, save those involving the pigment upon its outer border. The band of pigment was composed of dense masses of polygonal pigment granules within a fibrous tissue matrix and included many ova, all of which showed signs of degenerative changes. Ovary- and testis-portions were quite discrete but the line of demarcation was very irregular and the pigment appeared to ramify along the lines of the intertubular connective-tissues of the testis-portion. The anterior and middle lobes of the left gonad had a structure similar to the above, whereas the posterior lobe was entirely ovarian but pathological.

There was ciliated epithelium upon the peritoneum.

11. MARSHALL. (B.) *R. temporaria*. Adult. Killed during the winter. Secondary sexual characters typically male.

Right gonad. An ovo-testis having the appearance of an elongated and irregularly shaped testis bearing an irregular band of black pigmented material along the anterior two-thirds of the anterior border, and

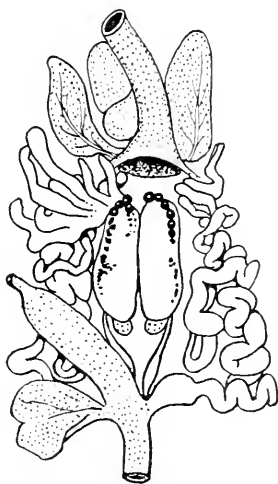


Fig. 11.

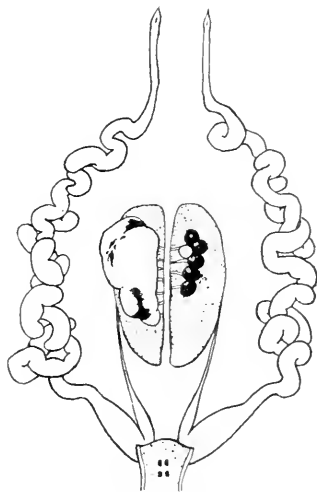


Fig. 12.

at the anterior pole, a clump of spherical bodies strongly pigmented and closely resembling ova in appearance. At the extreme anterior end there was a pigmented lobe separated from the main body of the gonad by a deep constriction.

Left gonad. An ovo-testis similar in appearance to the right save that there was no pigmented lobe at the anterior pole.

Vasa efferentia on both sides as those of the normal male.

Seminal vesicles small and spindle-shaped.

Müllerian ducts well-developed.

On section, the greater part of each gonad had the structure of normal testis, but ova were found in considerable numbers lying between the seminal tubules. The great majority of these ova were immature and showed signs of degenerative changes. The pigmented bands were composed of densely packed granules of pigment and hyperplastic connective-tissue. The anterior lobe of the right gonad consisted partly of normal testicular tissue and partly of ova in a state of extreme degeneration. The ovarian tissues were not discrete from the spermatogenic and were pathological.

12. CREW. (3.) *R. esculenta*. Adult. Killed November. Secondary sexual characters typically male.

Right gonad. An ovo-testis having the appearance of an irregularly shaped testis with bands of dense black pigmented material running in deep grooves along its twisted outer border.

Left gonad. An ovo-testis, consisting of six lobes, five of which were ovarian, and the other, testicular in appearance. The testicular lobule was placed centrally and medially in relation to the others.

Vasa efferentia, of the ordinary male pattern on the right: on the left four in number and connected with both ovarian and spermatogenic lobes of the gonad.

Seminal vesicles present but small and spindle-shaped.

Müllerian ducts well-developed.

On section, all those parts of the right gonad not including pigment had the structure of normal testis. The pigmented nodules consisted of densely packed polygonal masses of pigment granules and hyperplastic connective-tissue. No ova were found amid this pigment, but near to this two ova were seen lying between the seminal tubules of the spermatogenic tissue. The pigment had the appearance of following the lines of the intertubular connective-tissue. The left gonad consisted of two distinct portions. The five pigmented lobes were composed of pathological ovarian tissue in which degenerate ova were included among dense polygonal masses of pigment and hyperplastic connective-tissue. The spermatogenic lobe, discrete from the rest, was entirely testicular in structure. The renal vessels of both sides lay in deep pigmented channels upon the surface of the kidneys and the pigment was identical microscopically with that of the ovarian-portions of the ovo-testes.

13. RIDGEWOOD. *R. temporaria*. In first year. Killed November. Secondary sexual characters typically male.

Right gonad. An ovo-testis having the appearance of an exceptionally large testis bearing a small pigmented excrescence antero-externally.

Left gonad. An ovo-testis with a 3-lobed ovary-portion situated externally.

Vasa efferentia as those of the normal male.

Seminal vesicles present.

Müllerian ducts well-developed, more especially the left.

No sections were made.

14. CREW. (4.) *R. temporaria*. Adult. Killed May. Secondary sexual characters typically male.

Right gonad. An ovo-testis which save for a small pigmented pit upon the outer border had the appearance of a testis.

Left gonad. An ovo-testis having the appearance of an irregularly shaped testis which bore along its outer border a prominent pigmented crest, jet-black in colour and consisting of four spherical nodules in its anterior part.

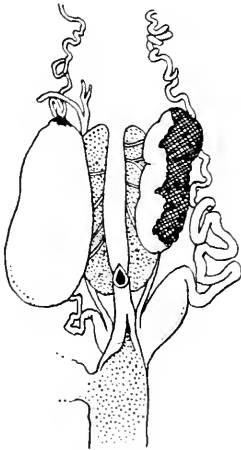


Fig. 13.

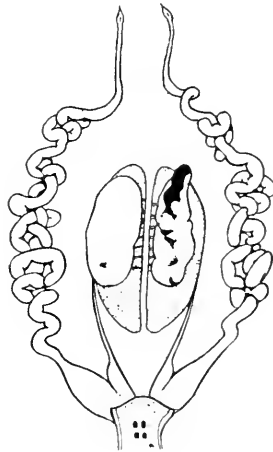


Fig. 14.

Vasa efferentia on both sides as those of the normal male.

Seminal vesicles well-defined.

Müllerian ducts moderately well-developed.

On section, the greater part of the right gonad had the structure of normal testis. Sections involving the pigmented pit showed the presence

therein of polygonal masses of pigment and broken down granular material. The left gonad was mainly spermiatic in structure but the pigmented parts consisted of masses of pigment, hyperplastic connective-tissue, and a few very degenerate ova. There was ciliated epithelium upon the peritoneum.

Group C. Those cases in which, on inspection, one gonad was an ovo-testis and the other a testis.

Sub-group 1. The testis was abnormal in appearance.

15. OGNEW. *R. temporaria*. Adult. Secondary sexual characters typically male.

Right gonad. An exceptionally large testis.

Left gonad. An ovo-testis with a small ovarian portion placed laterally.

Seminal vesicles were present.

Müllerian ducts. Right one moderately, left one well-developed.

No sections were made.

16. COLE. *R. temporaria*. Young and apparently immature. Killed during the summer. Secondary sexual characters typically male.

Right gonad. A testis somewhat enlarged and non-pigmented.

Left gonad. An ovo-testis with a larger densely pigmented ovary-portion and smaller non-pigmented papilliform testis-portions at its poles.

Vasa efferentia typically male on the right: on the left, only two but "the divisions of the renal artery to the ovo-testis might well have been mistaken for efferent canals."

Seminal vesicles not present.

Müllerian ducts. That of the right side was rudimentary and not convoluted, but had a distinct and densely pigmented uterine segment. That of the left side was pigmented, convoluted, and moderately well-developed, although its uterine segment was non-pigmented.

On section, the right gonad was a normal testis and with the exception of one small spherical patch and two or three problematical granular bodies, similar to those found in the opposite ovo-testis, pigment was entirely absent. One ovum at "a stage of development corresponding to that found in female frogs of between one and two summers" was found near the surface close to the junction of the anterior and middle thirds of the gonad, and the neighbouring portions of the testis were less conspicuous than the remainder of the gland and contained the most immature spermatozoa.

The left gonad was "for the most part made up of the polygonal pigment cells which occur normally in the frog's ovary, with, however, patches of normal testis at its poles. The anterior pole consists of testis with a thin zone of the pigment cells invading one side, whilst the posterior pole is somewhat over half testis. The remainder of the gland is occupied by the pigment cells alone. Further a horizontal section through the middle of the gland of this side, exposed five circular spaces in the pigment mass, containing, surrounded by fibrous capsules, spherical masses of lightly pigmented granular matter. Three out of the five completely filled their respective spaces—the other two did not, one of the latter also containing a large vacuole. The significance of these bodies, which may be free or lie indiscriminately among the pigment cells, and of the abnormally developed pigment mass, is, of course, on the available data, impossible to determine. The former may plausibly be looked upon as disintegrated ova (undergoing resorption)—the latter as preceding the development of ova and the formation of a true ovo-testis."

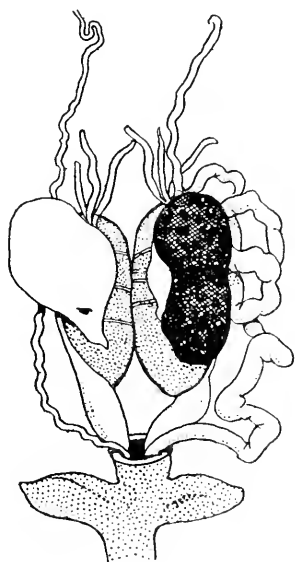


Fig. 15.

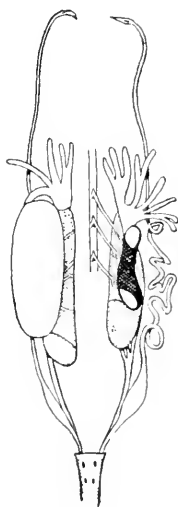


Fig. 16.

17. KENT. *R. temporaria*. Adult. Killed January. Secondary sexual characters typically male.

Right gonad. An ovo-testis consisting of an inner testis-portion divided by a well-defined transverse constriction into anterior and

posterior halves, and bearing along the anterior part of its outer border the strongly pigmented ovary-portion.

Left gonad. A testis of unusual shape.

Vasa efferentia of the male pattern present on both sides.

Seminal vesicles were present but were of unequal development, the left one being the larger.

Müllerian ducts. The right one was well-developed and much convoluted, but its uterine segment was small and non-pigmented. The left one was rudimentary and straight, but possessed a well-defined though small non-pigmented uterine segment.

On section the right gonad was seen to be composed of two discrete portions. The testis-portion consisted everywhere of normal spermatie tissue, but the ovarian was pathological. The left gonad was spermatie in structure, but throughout the gland ova were found some within and others between the seminal tubules. The presence of an ovum within a tubule was associated with deformity of the spermatozoa, which were obviously compressed. The presence of an ovum between seminal tubules was associated with fibrous overgrowth in the intertubular connective-tissue, and this produced deformity of the tubules in the neighbourhood. There was ciliated epithelium upon the peritoneum.

18. HUXLEY. (2.) *R. temporaria*. Adult. Killed October. Secondary sexual characters typically male.

Right gonad. An irregularly shaped testis with uneven outlines and a scarred surface.

Left gonad. An ovo-testis. A three-lobed testis-portion twisted upon itself, bore a prominent crest of pathological ovarian tissue upon its outer border.

Vasa efferentia of the usual male pattern on both sides.

Seminal vesicles were present but were small and fusiform.

Müllerian ducts. Right one weakly developed and convoluted and with a well-defined and pigmented uterine segment. The left one was well-developed.

On section, the right gonad had the structure of ordinary spermatie tissue save that six ova were found, two actually within and the rest between seminal tubules. Some of these ova had a normal appearance, others were degenerate. Accumulations of pigment, ovarian in origin, were found also between seminal tubules.

The left gonad consisted of an inner normal testis-portion and an outer pathological ovary-portion. The two were quite discrete and the ovary-portion contained but few ova and all of these were degenerate.

The greater part of the ovary-portion was composed of polygonal masses of pigment and hyperplastic connective-tissue. The cavities of the lobulated ovary were obliterated by this pigment but the divisions of the lobules were still distinct on section. There were ciliated cells upon the peritoneum.

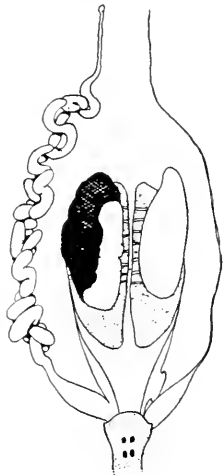


Fig. 17.



Fig. 18.

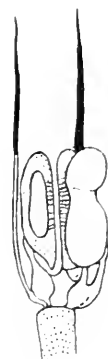


Fig. 19.

Sub-group 2. The testis was normal in appearance. None.

Group D. Those cases in which, on inspection, both gonads were testes.

Sub-group 1. The testes were abnormal in appearance.

19. LATTER. *R. temporaria*. Adult. Killed September. Secondary sexual characters typically male.

Right gonad. A faintly pigmented testis smaller than usual.

Left gonad. A faintly pigmented testis larger than usual and irregular in shape.

Seminal vesicles present.

Müllerian ducts only slightly developed, not convoluted, and solid in their anterior portions, but expanded in their posterior portions.

On section, ova were found in both testes, some within and others between the seminal tubules. Besides these ova degenerate cell-masses were found in similar situations.

20. MITROPHANOW. *R. esculenta*. Young. Secondary sexual characters male.

Right gonad. A testis much smaller than usual.

Left gonad. A testis smaller than usual.

Seminal vesicles present and well-developed.

Müllerian ducts well-developed.

On section, the right gonad contained one true ovum and many doubtful ones. A lobe at the anterior pole of the gonad was regarded as a rudimentary Bidder's organ. The true ovum lay within a seminal tubule. The left gonad was also a testis but contained doubtful ova only.

21. PEDASCHENKO. *R. temporaria*. Adult. Secondary sexual characters typically male.

Both gonads missing.

Müllerian ducts well-developed.

22. MARSHALL. (E.) *R. temporaria*. Adult. Secondary sexual characters typically male.

Both gonads missing.

Seminal vesicles present.

Müllerian ducts well-developed.

23. HOOKER. (A.) *R. fusca*. Adult. Secondary sexual characters typically male. Killed April.

Left testis missing.

Seminal vesicles small.

Müllerian ducts weakly developed with narrow uterine segments.

24. MARSHALL. (C.) *R. temporaria*. Adult. Secondary sexual characters typically male.

Right testis replaced by fat.

Vasa efferentia normal on the left; absent on the right.

Seminal vesicles present.

Müllerian ducts well-developed.

Sub-group 2. The testes were normal on inspection.

25. MARSHALL. (A.) *R. temporaria*. Adult. Secondary sexual characters typically male.

Seminal vesicles were small.

Müllerian ducts well-developed.

26. GERHARTZ. *R. esculenta*. Adult. Secondary sexual characters typically male. In addition to the usual male accessory sexual apparatus, well-developed Müllerian ducts were present.

27. TARNANI. *R. esculenta*. Adult. Secondary sexual characters typically male.

Seminal vesicles were not present.

Müllerian ducts were only moderately developed.

28. TICHOMIROW. *R. esculenta*. In an otherwise normal male moderately well-developed Müllerian ducts were present.

29. SUTTON. *R. temporaria*. In an otherwise normal male, slightly developed Müllerian ducts were present.

30. KORTSCHAGIN. *R. esculenta*. In an otherwise normal male, slightly and imperfectly developed Müllerian ducts were still present. The right one had separate anterior and posterior portions, it had no anterior opening and was solid.



Fig. 25.

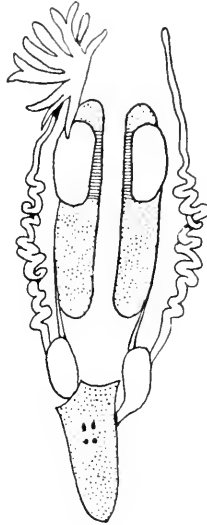


Fig. 31.

31. SUMNER. (1.) *R. virescens*. Adult. In an otherwise normal male, Müllerian ducts slightly developed and with no anterior openings were present.

32. SUMNER. (2.) *R. virescens*. Adult. In an otherwise normal male, very slightly developed Müllerian ducts with no posterior openings were present.

B. BUFO.

DIVISION II. SECONDARY SEXUAL CHARACTERS TYPICALLY MALE.

Group A. On inspection one gonad an ovary, the other an ovo-testis.

Sub-group 2. The ovary abnormal in appearance.

33. CERRUTI. (A.) *Bufo vulgaris*. Adult. Killed January. Secondary sexual characters typically male. (When captured was actually in copulation with a large female and appeared strongly excited.)

Right gonad. From behind forwards this consisted of (1) a pyriform testis-portion; (2) an ovary-portion; and (3) a Bidder's organ.

Left gonad. Posteriorly, an anomalous ovary; and in front of this, a Bidder's organ.

Vasa efferentia. "Serial sections revealed the lack of a *rete testis*."

Müllerian ducts. Right one relatively long and thin, terminating blindly; left one relatively shorter and also terminating blindly. On section the testis-portion of the right gonad showed the presence of sperms of normal appearance mingled with other cellular elements having variable form and size, "many of which are to be considered as spermatids or spermatocytes in more or less advanced stages of degeneration." The intercanalicular connective-tissue was abundant around the tubules towards the centre of the testis-portion, and between the tubules were numerous cells pigmented yellowish-brown.

The ovarian tissue of both gonads presented common characters. The smaller oocytes presented a normal structure but the larger ovules exhibited signs of degeneration and contained numerous granules of yellow-brown pigment.

Since the Müllerian ducts ended blindly, the ova, even if produced, could not be emitted.

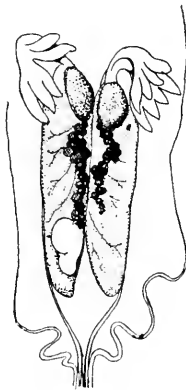


Fig. 33.

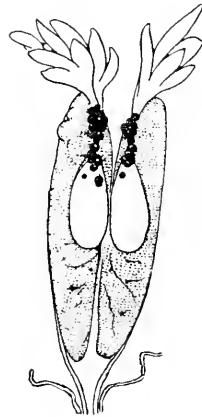


Fig. 34.

Group B. On inspection both gonads ovo-testes.

34. CERRUTI. (B.) *Bufo vulgaris*. Adult. Secondary sexual characters not described.

Right gonad. Posteriorly, a pyriform testis-portion; anteriorly, an ovary-portion. From the anterior part of the testis-portion "one sees

projecting from the testicular stroma some ovules of notable size and browned with darkish pigment." Bidder's organ missing.

Left gonad. Similar to the right.

Vasa efferentia. "Relation to the kidneys normal."

Müllerian ducts had been cut away before the examination was made. On section the testis-portions had the normal structure. The ovules seen projecting from the testicular stroma were in an advanced stage of degeneration, being full of a granular substance—"in which are present numerous granules of a yellowish-brown pigment and a rare nucleus belonging to immigrant cells (perhaps leucocytes)." The ovary-portions contained ova of all stages of development. The young and medium were mostly normal though "in some the cytoplasm does not appear homogeneous but in sections presents striae which stain deeply with acid dyes. The nucleoli appear homogeneous or vacuolated and the chromatic threads stain with great difficulty." "The larger ova 850-900 M. seem like normal coocytes of equal size, but sections of them show easily that they are in a very advanced stage of degeneration, being invaded by immigrant elements, probably leucocytes, and containing numerous granules of yellow-brown pigment."

(In one figure is shown a dark mass due to an accumulation of granules of normal yellow-brown pigment, which Cerruti suggests represents an egg in a more advanced stage of degeneration.)

35. SPENGLER. *Bufo cinereus (vulgaris)*. Adult. Secondary sexual characters typically male.

Each gonad consisted from behind forwards of a testis-portion, an ovary-portion of several ovarian chambers and containing ova as large as those seen in a female of 2 or 3 years.

36. KNAPPE. *Bufo vulgaris*. Adult. Secondary sexual characters typically male.

Each gonad consisted from behind forwards of a testis-portion, a Bidder's organ, an ovary-portion, another Bidder's organ.

37. KING. *Bufo lentiginosus*. Adult. Killed March. Secondary sexual characters male.

Right gonad. An ovo-testis with testis-portion posteriorly. No Bidder's organ.

Left gonad. An ovo-testis, similar to that of the right side. The ovary was placed where normally the Bidder's organ would have been.

Vasa efferentia present.

Müllerian ducts still present but without terminal dilatations.

On section, the testis-portions had the structure of normal spermatie tissue; while all the larger ova within the ovary-portions showed degenerative changes.

Group D2. Both gonads testes, normal in appearance.

38. SPENGEL. *Bombinator igneus*. Adult. In an otherwise normal male, the right Müllerian duct was as well-developed as the oviduct of a female and the left, though smaller, was abnormally large.

C. PELOBATES.

DIVISION II. SECONDARY SEXUAL CHARACTERS TYPICALLY MALE.

Group C2. On inspection one gonad an ovo-testis, the other a testis of normal appearance.

39. SPENGEL. *Pelobates fuscus*. Adult. Secondary sexual characters typically male.

Right gonad. A normal testis.

Left gonad. An ovo-testis of which the posterior part consisted of a 2-lobed ovary, containing pigmented ova of the size of normal mature ova.

Accessory sexual apparatus as that of a normal male.

Müllerian ducts extremely rudimentary.

D. HYLÆ.

DIVISION II. SECONDARY SEXUAL CHARACTERS TYPICALLY MALE.

Group D2. Both gonads testes, normal in appearance.

40. SWEET. *Hyla aurea*. Adult. Secondary sexual characters typically male.

Right and left gonads both testes normal in appearance.

In addition to the usual male accessory sexual apparatus, Müllerian ducts were present, being well-developed, but having no posterior openings.

On section, ova were found within both testes.

The species and the extent of the abnormality.

The species which contributed the abnormalities and the nature of the abnormality are shown in the following Table:

TABLE I.

DIVISION I.				<i>R. temporaria</i>	<i>R. esculenta</i>	<i>R. fusca</i>	<i>R. virescens</i>	<i>Bufo vulgaris</i>	<i>Bufo lentiginosus</i>	<i>Pelobates fuscus</i>	<i>Bombinator igneus</i>	<i>Hyla aurea</i>	Totals
The secondary sexual characters were not typically male													
Group A.	One ovary ; one ovo-testis										—
Sub-group 1.	The ovary was normal in appearance	2	—	—	—	—	—	—	—	—	2
Sub-group 2.	The ovary was abnormal in appearance	3	—	—	—	—	—	—	—	—	3
Group B.	Two ovo-testes	1	—	1	—	—	—	—	—	—	2
Group C.	One ovo-testis ; one testis										—
Sub-group 1.	The testis was abnormal in appearance	—	—	—	—	—	—	—	—	—	0
Sub-group 2.	The testis was normal in appearance	—	—	—	—	—	—	—	—	—	0
Group D.	Two testes										—
Sub-group 1.	The testes were abnormal in appearance	—	—	—	—	—	—	—	—	—	0
Sub-group 2.	The testes were normal in appearance	—	—	—	—	—	—	—	—	—	0 = 7
DIVISION II.													
The secondary sexual characters were typically male													
Group A.	1. As above	—	—	—	—	—	—	—	—	—	0
„	2. „	—	—	—	—	1	—	—	—	—	1
Group B.	„	5	1	1	—	3	1	—	—	—	11
Group C.	1. „	4	—	—	—	—	—	—	—	—	4
„	2. „	—	—	—	—	—	—	1	—	—	1
Group D.	1. „	4	1	1	—	—	—	—	—	—	6
„	2. „	2	4	—	2	—	—	—	1	1	10 = 33
Totals				21	6	3	2	4	1	1	1	1	
				32			5			1	1	1	= 40
Group A ... 6				Group C ... 5									
„ B ... 13				„ D ... 16									

Of the 40 cases described, 21 were furnished by *R. temporaria*. This does not mean, necessarily, that this species is more prone to abnormality than any other, however, and the explanation of these figures possibly lies in the fact that the Common Grass Frog is used for laboratory purposes more commonly than others. Only 40 cases have been thought worthy of detailed description, but there is little doubt that similar cases have been encountered in every Zoological Laboratory though unrecorded. Nevertheless, such abnormality must be regarded as very rare, though certainly occurring in all species of the Anura.

The primary sex-glands of these abnormal individuals.

Spermatic and ovarian tissues were present, as noted in the tabulated List of Cases, separately and in combination, in the following grades.

Sp. Spermatic tissue. Ov. Ovarian tissue. ? Details not available. ♂ As in the male.
 ♀ As in the female. - Less than. -- Much less than. --- Very much less than.
 Abs. Absent. Rt Right. Lt Left.

Case	Right gonad		Left gonad		Vasa efferentia	Seminal vesicles	Müllerian ducts
	Sp.	Ov.	Sp.	Ov.			
A.	I A 1	1	—	1	1	+	+
	2	1	—	2	+	+	+
	A 2	3	—	2	2	Rt + : Lt - - ♂	- -
	4	—	3	1	3	-	-
	5	1	3	—	3	Rt - : Lt - ♂	-
	B	6	1	2	1	2	-
	7	?	?	?	?	?	Rt - : Lt - ♀
	II B	8	1	1	1	1	-
	9	1	3	2	?	?	-
	10	1	3	1	3	3	-
	11	2	3	2	4	4	-
	12	2	4	1	3	Rt : Lt - ♂	-
	13	?	?	?	?	?	-
	14	1	4	1	3	3	-
C	1	?	—	?	?	?	Rt - : Lt -
	16	2	—	1	3	3	Rt - : Lt -
	17	1	3	2	—	—	Rt - : Lt -
	18	2	—	1	3	3	Rt - : Lt -
D	1	2	—	2	—	—	- -
	20	2	—	2	—	—	- -
	21	— Abs.	—	— Abs.	—	—	- -
	22	— Abs.	—	— Abs.	—	—	- -
	23	1	—	— Abs.	—	—	- -
	24	— Abs.	—	1	—	—	- -
	D 2	25	1	—	1	—	- -
D 2	26	1	—	1	—	—	- -
	27	1	—	1	—	—	- -
	28	1	—	1	—	—	- -
	29	1	—	1	—	—	- -
	30	1	—	1	—	—	- -
	31	1?	—	1?	—	—	- -
	32	1?	—	1?	—	—	- -
B.	II A 2	33	2	2	2	2	- -
	II B	34	1	2	1	2	- -
	35	?	?	?	?	?	- -
	36	?	?	?	?	?	- -
	37	1	2	1	2	2	- -
II D 2	38	1	—	1	—	—	Rt + : Lt - ♀
C.	II C 2	39	?	—	?	?	?
D.	II D 2	40	2	—	2	—	- -

Spermatic tissues.

1. Normal healthy spermatic tissue (represented as Sp. 1).
2. Healthy spermatic tissue with ova and pigment included within its structure. (Sp. 2.)

Ovarian tissues.

1. Normal healthy ovarian tissue. (Ov. 1.)
2. Ovarian tissue in which a considerable proportion of the ova were degenerate and in which there was overgrowth of the connective-tissue and an increase of the pigment. (Ov. 2.)
3. Ovarian tissue in which the degenerative changes were more pronounced, the ova being all degenerate and the hyperplasia of the connective-tissue and the density of the pigment being more marked. (Ov. 3.)
4. Ovarian tissue in the extreme stages of degeneration. No ova remained and all that was left was a nodular mass of pigment and fibrous tissue. (Ov. 4.)

Using these grades, it is possible to arrange the cases as on p. 162.

Reviewing only the cases of abnormality in *Rana* it is seen that the various forms of ovarian and spermatic tissues furnish gonads as follows :

Case and gonad										Totals
Ov. 1	1 Rt...	1
Ov. 2	3 Rt, 2 Lt	2
Ov. 3	4 Rt, 5 Lt	2
Ov. 4	Nil	0 = 5
Sp. 1	23 Rt, 24 Lt, 25—32 both	18
Sp. 2	16 Rt, 17 Lt, 18 Rt, 19 and 20 both	7 = 25
Sp. 1, Ov. 1	11 Lt, 8 both	3
Sp. 1, Ov. 2	2 Rt, 6 both	3
Sp. 1, Ov. 3	5 and 9 Rt, 4 Lt, 10 both, 12 Lt, 14 Lt, 16 Lt, 17 Rt, 18 Lt	10
Sp. 1, Ov. 4	14 Rt	1 = 17
Sp. 2, Ov. 1	Nil	0
Sp. 2, Ov. 2	3 Lt	1
Sp. 2, Ov. 3	11 Rt	1
Sp. 2, Ov. 4	11 Lt, 12 Rt	2 = 4
In the case of 13 gonads sections could not be or were not made										13 13
Total										64
One gonad	The other		Case	Totals						
Ov. 1	Sp. 1, Ov. 1		1	1						
Ov. 2	Sp. 1, Ov. 2		2	1						
Ov. 2	Sp. 2, Ov. 2		3	1						
Ov. 3	Sp. 1, Ov. 3		5 and 6	2						
Sp. 2	Sp. 1, Ov. 3		16, 17, 18	3						

When the abnormalities of the reproductive system are thus arranged in a graduated series, they appear to be merely phases of one process at the beginning of which the gonad has the appearance of a normal typical ovary, and at the end of which the same gonad is in every way a typical testis. At the beginning, the gonad is an ovary of considerable size, and is capable of functioning as such and of producing mature ova (Case 1 Rt); it contains many ova in various stages of development, and a considerable amount of undifferentiated germ-tissue, much of which is situated upon the inner border of the gonad. Then upon this inner border, one or several patches of spermatie tissue make their appearance (Cases 3 and 4 Lt). These have developed from the hitherto undifferentiated germinal tissue of this region. Very soon after this, the ovarian tissue of both gonads begins to show signs of degenerative changes, such as an increase in the relative amount of pigment, a diminution in the size of the nuclei of the ova, and a shrinking of the cytoplasm with vacuolation (Case 2). The spermatie tissue progressively increases in amount, and the ovarian undergoes progressive degeneration, becoming less and less in amount, and more and more solid in consistence, while the pigmentation becomes more and more intense. Fewer and fewer ova are found within its shrinking bulk (Cases 4 Lt, 5 Rt), until at length the gonad assumes the form of a testis irregular in shape, and with its surface scarred with deep grooves, which bears upon its outer border a sub-peritoneal crest of jet-black nodules of pigment cells and fibrous tissue (Case 14 Rt). This pigment, now a harmful foreign body, is slowly removed by the blood-stream, and can be identified within the renal veins, and the testis, becoming healed, ultimately assumes the form and appearance of the normal gonad of the typical male (Cases 25-32).

It seems clear that at the beginning one gonad—usually the right—is the seat of this transformation, for when both gonads are affected, they exhibit two different phases of the process, that in one being more advanced than that in the other, and it seems that the occurrence of this phenomenon in one gonad favours its onset in the other. Since the degeneration of the ovarian tissue is often equally pronounced in the ovary of the opposite side, it is reasonable to assume that in every case in the lists, both gonads have been, are, or would have been affected.

Ova are often found amid the spermatie tissues of the testis-portion of an ovo-testis and of an otherwise normal testis. Normally ova are extruded from the surface of an ovary. In an ovo-testis they are extruded from the ovarian portion into the testis-portion (or the actively

growing spermatie tissues envelop ova and pigment along the line of junction of ovary—and testis-portions), where they remain more or less healthy for a considerable time, resisting destruction by virtue of their maturity and being nourished and protected by the surrounding tissues, while the other ovarian structures are destroyed and removed. The presence of such ova is sufficient indication that the testis which includes them has been an ovo-testis. These ova are doomed and ultimately become resorbed, leaving the testis perfectly normal.

The question as to whether these ova are to be found actually within the seminal tubules is of some importance, since if they are found in this situation, it is not unreasonable to suggest that such cells may be the results of the division of spermatogonia. There is, however, no reason why ova produced by the ovary-portion of an ovo-testis should not be found within a seminal tubule of the testis-portion of the gonad, and if these cells are also found between the tubules, then force is given to the contention that they are ova, and that they are the products of ovarian and not of spermatie tissue.

When such an ovum is found within a seminal tubule, the spermatozoa also present therein are greatly compressed. The ovum thus may have the normal structure, while the spermatozoa may be deformed and degenerate. But this degeneration is the result of local pressure, and is not an indication that the ovarian tissue generally is healthy and spermatie degenerate. When the ovum is situated between the seminal tubules, those in the neighbourhood are contorted and misshapen. This is the result of local hyperplasia of the intertubular connective tissue, which follows the irritation set up by the presence of the foreign body—the ovum and its pigment.

It is seen that Ov. 4 type ovarian tissue does not occur alone, but only in association with spermatie tissue. Sp. 1 tissue is such as is found in the very earliest stages, and in the closing stages of this process: in the first it is associated with type Ov. I ovarian tissue. But in the closing stages, ova which have been extruded from the ovarian tissues, so that these are such as have been designated by the formula Sp. 2, and all that remains of the other ovarian tissues, is the pigment which is massed along the outer border of the gonad.

There is no gonad with the constitution Sp. 2, Ov. 1. This is because in the case of type Ov. 1 ovarian tissue, there is, as yet, no appreciable degeneration and no considerable degree of growth on the part of the spermatie tissue. It is by the active enveloping growth of the spermatie tissue that ovarian ova and pigment become included within them.

In those cases in which one gonad was a testis and the other an ovo-testis, it is seen that the tissues of the testis are of the formula Sp. 2. This definitely proves that the testis, which contains ovarian pigment and ova, is a gonad in which the transformation from ovary to testis is more advanced than in the gonad of the opposite side.

Although the process may begin in either gonad apparently, yet in the 18 cases in which anything approaching a true estimate can be made, the right gonad was first affected in 13 cases: the left one in 5 only.

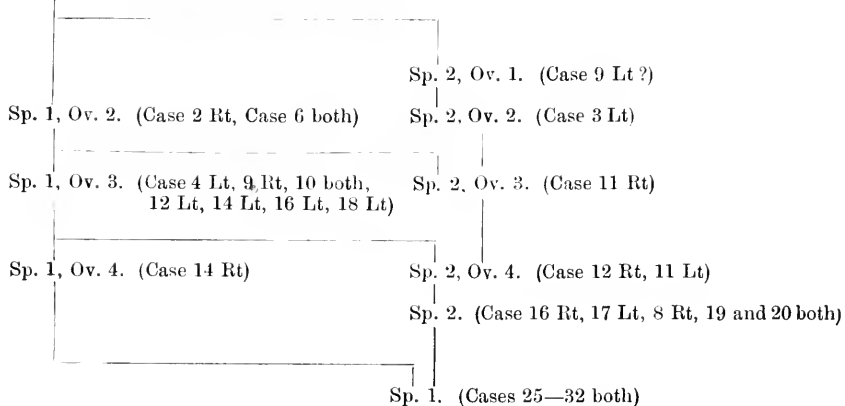
It is the rule that the testis-portion of an ovo-testis is situated upon the inner border of the gland, a position in every way convenient for its association with vasa efferentia. The ovary-portion is always placed externally to the testis-portion—and this fact has to be remembered when the question as to whether a crest of pigment containing no ovum is ovarian tissue or not is raised.

It would seem then, that if spermatic tissue becomes developed in a gonad which previously has possessed the characters of an ovary, it makes its appearance in a definite situation. This points to a localisation in the germinal tissue.

The process thus outlined can be depicted graphically by the use of the formulae employed above. (Ov. 1, it will be remembered, is ovarian tissue which, on microscopical examination, has the normal structures.)

Ov. 1. (Case 1 Rt)

Sp. 1, Ov. 1. (Case 1 Lt, and Case 8 both)



The degenerative changes in the ovarian tissue of both gonads quickly follow the development of spermatic tissue in one and the degree of this degeneration is more or less equal on the two sides. There is no

case in which the ovarian tissue was thoroughly healthy in one gonad whilst degenerate in the other. If the presence of the spermatic tissue in one gonad is responsible for the ovarian degeneration, then the agent which produces this must be blood-borne, after the manner of a hormone.

The Accessory Sexual Apparatus.

Vasa efferentia. It is seen that every gonad described as a testis, whether it was normal or abnormal, was equipped with these efferent ducts. The testis-portion of every ovo-testis also was linked up with its kidney, but in these cases the vasa efferentia were commonly reduced in number, when compared with the same structures of the typical male. In those cases in which one gonad was an ovary, the findings of different investigators have differed, but in some cases efferent ducts were found connecting up gonad and kidney. Similarly, in the case of an ovo-testis, vasa efferentia were found, not only in connection with the testis but with the ovary-portion of the gonad too. Spermatic tissue in a gonad, therefore, is invariably equipped with vasa efferentia, even though its amount is relatively small, and ovarian tissue of an ovo-testis and of an ovary is frequently found to be supplied with these efferent ducts. The less the relative amount of spermatic and the greater the amount of ovarian tissue in the gonads, the less likelihood there is that vasa efferentia of the male pattern will be found.

It is very exceptional to find any suggestion of efferent ducts in a typical female. During the examination of many hundreds of individuals, no trace of such has been found. Therefore, it is reasonable to assume that whilst the gonads have the constitution represented by the formula Ov. 1, no efferent ducts will be present, and that they make their appearance at the time of the early growth of the testis-portion of the ovo-testis (Sp. 1, Ov. 1), and thereafter keep pace with the development of the testis.

The seminal vesicles. These were absent in 5 cases (1, 2, 5, 7, and 8), and less developed than in the typical male in 10 others (3, 4, 6, 9, 11, 12, 16, 18, 23, and 25). Most of these occur towards the beginning of the table, so that the nearer the individual approximates with respect to the nature of the gonads, and to the nature of the secondary sexual characters, to these characters in the typical female, the more likely are the seminal vesicles to be either smaller than those of the typical male or even absent altogether. Conversely, as has been pointed out previously, in those cases in which the gonads and the secondary

sexual characters generally approximated those of the typical male, the seminal vesicles were also, almost without exception, as those of the typical male.

These facts suggest that there is some definite relation between the nature of the gonads and the development of the accessory reproductive apparatus. Cole's conclusion that "a good diagnostic feature as regards sex is the seminal vesicle, which has only been observed in hermaphrodites predominantly male" is justified, for it is seen that the vesicles are commonly poorly developed or absent altogether in those cases in the lists which were more female than male as regards their secondary sexual characters and the nature of their gonads, in which a considerable amount of ovarian tissue was present. In several cases the vesicles were small or absent although there was no ovarian tissue present in the gonads which were composed entirely of spermatie tissue. In most of these cases unfortunately, the age of the individual and the season of the year are not stated, and consequently a true estimate of the importance of the condition of the vesicles cannot be made. Reviewing the whole of the cases, however, it is seen that there is some connection between the development of the seminal vesicles, and of the vasa efferentia also, and the presence of spermatie tissue in the gonads.

In this connection, it is noteworthy that Nussbaum in 1905 found that the size of the seminal vesicles was controlled by the internal secretion of the testis.

It will be noticed that the degree of development of the seminal vesicles and that of the vasa efferentia are connected, for in Cases 1, 2, 3, 4, 5, 7, 12, both of these structures differ in degree of development from those of the typical male, in that both were poorly developed. Whatever affects the development of the one, therefore, also affects that of the other.

Müllerian ducts. The degree of the development of these typically female ducts in the cases tabulated varies from almost the rudimentary condition normally found in the typical male—fine straight strands of tissue as described by Müller, Burro, and Rathke—to that of the fully developed oviduct of the typical adult female. In 18 cases these ducts were found to be well-developed, moderately well-developed in 2, slightly or weakly developed in 6, in 5 other cases the development of the ducts of the two sides was unequal.

It will be seen that it is the rare exception for these ducts to be anything but well-developed in those cases in the first half of the table, that is, in those cases in which a considerable amount of ovarian tissue

still was present, and further that towards the end of the table the condition of those ducts is more and more frequently described as moderately, slightly or weakly developed. In the last 14 cases, the ducts were well-developed in 6, moderately developed in 2, and slightly developed in 6, and in all these only spermatic tissue was present in the gonads.

So that in an otherwise normal male, Müllerian ducts in form and size equal to the oviducts of the adult female are found in the presence of actively functioning spermatic tissue. Harms and Meisenheimer claim to have demonstrated that the internal secretion of the male gonad can encourage the development of the accessory reproductive apparatus of the opposite sex, and if this is so, then in such cases the unusual development of the Müllerian ducts may have been a response to the action of the internal secretion of the testes. Experiments conducted to test the findings of Harms and Meisenheimer have failed to confirm their results, and there is reason to believe that the occurrence of Müllerian ducts in form and size equal to the oviducts of a mature female, in an otherwise typical male, is an indication that functional ovarian tissue of considerable amount has been present in the gonads of the individual.

It is of interest to note that, in 1885, Sutton made the following generalisation:

“When a male frog develops a Bidder’s organ or ovary in conjunction with a testis, the Müllerian duct or oviduct then assumes some considerable size,” and from the results of the examination of more than 250 specimens of *R. temporaria* he concluded “that as a rule the amount of development of these ducts is in direct proportion to the size of the Bidder’s organ.”

It is gathered from the tables that the presence of spermatic tissue in the gonads is associated with a fuller development of vasa efferentia and seminal vesicles, and that the Müllerian ducts attain their fullest development only in the presence of ovarian tissue. It is suggested, therefore, that the presence of well-developed oviducts is, in itself, an indication that ovarian tissue either is or has been present in the gonads of the individual possessing them. When once they have attained a considerable size, as they do in association with the development of ovarian tissue, the oviducts persist, even though the ovarian tissue is removed. This can be demonstrated by extirpation of the ovaries, after which the oviducts retain their form and size certainly for several months. They do not attain a fuller development during the breeding-

season in cases thus operated upon, but they certainly do not atrophy. In the cases in the lists, it is seen that only in those in which there still remained some ovarian tissue capable of producing ova, though they were abnormal and degenerate, did the oviducts exhibit a seasonal increase in size and activity. In the majority their glandular portions still retained the power of manufacturing their particular secretion, for in water the ducts became much swollen, and this is a further proof that the ducts do not undergo any considerable degree of atrophy.

There is no evidence that the seasonal activity of the testis in these cases produces a corresponding increase in the size and activity of the Müllerian ducts, as would be expected from the results of the experiments of Harms and Meisenheimer. It is seen, as has been stated above, that this increase is only shown in those cases in which ovarian as well as spermatie tissue was present in the gonads.

It seems probable, therefore, that when the gonad has the constitution represented by the formula Ov. 1, oviducts become developed up to the female standard; that when the gonad's composition becomes that represented by Sp. 1, Ov. 1, vasa efferentia and seminal vesicles make their appearance; and that coincidently with the fuller development of the testis-portion of the ovo-testis, the male accessory reproductive apparatus attains the form and size of that of the typical male, while the oviducts, having reached a considerable size already, retain their form throughout the process which is converting a young female into a somatic male.

Granting that the hormones of the gonad are responsible for the stimulus which calls forth the development of the accessory reproductive apparatus, it is seen that the exhibition of the specific male hormones does not cause the development of any structure which is not represented embryologically in the normal female, and that hormones act merely by inhibition or stimulation of normal embryonic rudiments.

The Müllerian ducts were of unequal development in a few cases, and in these the better developed duct was on the side of the body on which more ovarian tissue was still present (cf. Aves).

Case	Right gonad		M.D.	Left gonad		M.D.
	Sp.	Ov.		Sp.	Ov.	
7	?	?	- ♀	?	?	♀
15	?	—	- ♀	?	?	♀
16	2	—	- ♀	1	3	- ♀
17	1	3	- ♀	2	—	- ♀
18	2	—	- ♀	1	3	♀

There is, therefore, some evidence that the degree of development of the Müllerian duct is controlled to some extent by the activity of the ovary of the same side. It would seem that the Müllerian ducts are developed under the direction of the ovaries, but that the degree of their development in these cases is determined by the time during general development at which the spermatie tissues first become expressed. If this is expressed relatively early, then these ducts will not have attained their full development, and their conditions will be as in Cases 14, 27, and 28. If spermatie tissue becomes expressed even earlier still, then the ducts will be as in Cases 20, 23, 29, 30, 31, and 32. If, on the other hand, this expression is relatively later, then the ducts will have already attained their full development and will retain their characters.

In the cases in which these ducts were of unequal development, it would seem that the process of transformation of ovary into testis began, as is usual, in one gonad, and later extended to the other, and that the interval between the beginning of the process in the two gonads was prolonged, so that the duct of the side on which spermatie tissue had yet to become expressed in the gonad would be permitted to develop a little further, as the ovarian tissue of this side would be affected to less extent than that of the other.

A point of interest arises in Cases 30, 31 and 32. In Case 32 these ducts had no posterior openings, while in the others they were solid in their anterior portions.

The Secondary Sexual Characters.

Of the 30 frogs in the tables of which sufficient details were given as to their secondary sexual characters 25 (83·3 %) were definitely and typically male. Four others were definitely but imperfectly male (13·3 %), and in the remaining case the secondary sexual characters were female (3·3 %).

In every case functioning spermatie tissue was present, and in those cases in which ovarian tissue was also present, and in which sufficient description of its histological structure was given, it has been shown that this tissue was pathological and undergoing removal.

The presence of imperfectly developed male secondary sexual characters is not associated with the development of female characters as is seen in Cases 2 and 4, and the secondary sexual characters can remain fully and typically male in the entire absence of the gonads, as is illustrated by Cases 21 and 22.

These characters do not become at all obvious while the individual is still young, and the female characters are, for the most part, negative in nature. Assuming that there is some intimate relation between the primary and secondary sexual characters, a review of the cases suggests that the super-imposition of male upon female secondary sexual characters is a simple matter in the Anura. The presence of patches of ciliated epithelium upon the peritoneum round about the suspensory ligament of the gonad does not interfere with the assumption of the male characters which are developed in quite different situations. The wartiness of the skin is a seasonal phenomenon and only occurs in the presence of functioning ovarian tissue.

It has been shown that the development of spermatic tissue upon the inner border of a gonad, which previously had every appearance of an ovary, occurs at an early stage in the life-history of the individual, and that coincidently with its appearance the ovarian tissue begins to degenerate. If, then, the female secondary sexual characters are not developed to any extent, until the normal female is well-matured, the development of the spermatic tissue in these abnormal individuals and the consequent destruction of the ovarian tissue will prevent the assumption of the female characters.

The degree of development of these characters bears no relation to the amount of germinal tissue present, but this tissue must be healthy and functioning. A small amount of healthy spermatic tissue is associated with well-defined male secondary sexual characters, although in the individual there is a greater amount of ovarian tissue which is pathological. It is seen that the exhibition of the male sex-hormones is not attended by the development of any structure which is not represented embryologically in the normal female, and that as in the case of the accessory reproductive apparatus, the hormones act by inhibition and stimulation of normal embryonic rudiments.

The cases of abnormality in *Bufo*, *Bombinator*, *Pelobates* and *Hyla* are too few to permit of a similar treatment to that adopted in the case of *Rana*. They are, however, exactly similar in their nature and there can be no doubt that the conditions found are, with minor differences, identical with those described in *Rana*.

The relative position of ovarian and spermatic tissues in an ovo-testis is somewhat different, in that the ovarian tissue is placed anteriorly and the spermatic posteriorly. Further, it would seem that the comparatively smaller amount of spermatic tissue is associated with the assumption of male, secondary, sexual characters in the case of *Bufo* than in *Rana*.

The gonad of *Bufo* is subject to considerable variation. Cerruti figures a *Bufo vulgaris* in which he observed, in front of each testis, a Bidder's organ, another piece of testis, another Bidder's organ and lastly the fat-body; and in another case, quoted in the lists, in which in place of Bidder's organ there was found in front of each testis an ovary. Knappe describes a case, quoted also in the lists, in which he observed in front of each testis a Bidder's organ, an ovary, another Bidder's organ and lastly the fat-body. King has dealt with such abnormalities at length, and she is of the opinion that the component cells of an embryonic testis or ovary, in response to the stimulus of altered blood supply, can assume the characteristics of a Bidder's organ. It certainly does appear that cells which normally should develop into typical testis or ovary or Bidder's organ can, on occasion, develop into another of these tissues.

In Cases 34 and 37 the position of the ovarian portion, coupled with the fact that the Bidder's organ was missing, strongly suggests that these had been derived, in part at least, from those cells which normally would have given rise to Bidder's organ. Further, as King points out, as the testis-portion in these cases was shorter than the normal testis of the typical male, it may be assumed that the primordial germ-cells in the anterior part of the germinal ridge, which normally would have developed into spermatie tissue, had also taken part in the formation of the ovary. She suggests that the causal agent, whatever it may have been, must have acted at a very early period in the life-history of the individual, since in the normal toad the cells which develop into Bidder's organ become differentiated when the tadpole is about two weeks old.

In Cases 33, 35 and 36, an ovary was found between the Bidder's organ anteriorly and the testis posteriorly. This can be interpreted as the condition in which the most anteriorly situated cells of the germinal ridge have developed, as is usual, into a Bidder's organ, those situated posteriorly into a testis, while the cells of the more anterior part of the middle region of the ridge have developed, for some reason or other, into an ovary. In Case 39 one gonad was an ovo-testis with the ovary-portion posteriorly situated. There is in this a strong suggestion that either the forerunners of testis, ovary, and Bidder's organ are normally present in the apparently undifferentiated primordial germ-tissue, or perhaps, that the foundation primordial germ-cells, in response to the appropriate stimulus, can become any one or all of the three types of adult germinal tissue.

The cases illustrate the process by which an individual with every female character ultimately comes to possess the typical male organisa-

tion. But these transformed individuals not only assume the male characters but also can behave and function as males.

The opportunity neglected by Cerruti (Case 33), of applying the test of breeding in order to examine the exact nature of an individual with an abnormal reproductive system, presented itself to me.

It can be assumed that in the frog sex-determination is effected by means of a sex-chromosome mechanism. The sex-chromosomes have not yet been demonstrated, but Huxley has given reasons for the belief that the chromosome-constitution of the frog is of the XY, XX type.

It so happened that the specimen referred to in the lists as No. 14, when received, was actually in copulation. This pair, with many others, was retained for breeding purposes. The individuals were marked and full details collected during the course of the breeding. Later, when the tadpoles had hatched, the parents were killed and dissected. Then it was that the abnormalities were first noticed and in consequence every attention was paid to the examination of the female with which this abnormal individual had mated and to the rearing of the offspring. The female proved to be normal in every way anatomically; she died before she could be bred from again.

The eggs and tadpoles resulting from this union were raised according to the directions given by H. D. King and every effort made to rear as many individuals as possible. The fertilised eggs from seven other couples were kept under exactly similar conditions to furnish controls.

The eggs nearer the centre of the egg-mass gave rise to few tadpoles and the eggs that were fertilised did not all hatch, for numbers of such were arrested in their development by death. The question of selective mortality naturally enters into a consideration of the sex-ratio of the individuals which did survive therefore. But there is no evidence to show that the sex-ratio would have been different if every egg had hatched and every tadpole had survived.

As the tadpoles passed the metamorphosis, they were removed to outdoor pens under conditions as natural as possible, the different lots being kept separate.

During twelve months, the frogs were examined in batches at intervals of two months. Every one that died was examined and included in the records. The controls showed no great variation in the relative numbers of the sexes and towards the end of the experiment only two lots were maintained.

The gonads were sectioned and compared to the standards given by Witschi. No case of the indirect method of development of a testis was

encountered, the gonads were either ovary or testis or else the tissues were too undifferentiated to allow of a decision being made. In all 2356 tadpoles and frogs were examined.

But of the frogs which resulted from the union of the male with the abnormal reproductive system and a normal female, every one of the 774 examined and found with gonads sufficiently developed was a female normal in every respect. Those of the control lots were typically male or female and no case of abnormality was met with among them. The relative numbers of males and females varied in the different lots but only to a slight degree, the average being 46% males, 54% females. The average of all the lots was 23% males and 77% females, which was distinctly different from the figures of the parental generation (80% males and 20% females), constituting, in fact, a very complete swing-back.

The results of this breeding experiment go far to prove that the male parent was a "somatic" male, a masculinized female. Though possessing the male organisation yet in chromosome-constitution it was a female (XX), and when mated to a normal female (XX) produced a generation consisting entirely of females. Its chromosome-constitution had become over-ridden by external factors.

There is considerable evidence, as Huxley recently has shown, that chromosome-constitution may thus become over-ridden. He cites the work of Goldschmidt who lately has bred from ZW males and from ZZ females of *Lymantria*, and that of Shull, Strasburger, and Doncaster on *Lychnis dioica*.

Lillie's work on the free-martin can be interpreted as further proof that in the female—presumably XX in chromosome-constitution—embryos in cattle, co-twins of males, the whole organisation can be so altered that even the gonad itself takes on the characters of testis and the accessory sexual apparatus becomes more male than female.

Doncaster in one of his latest papers suggested that the sterile tortoiseshell tom-cat possibly is a female chromosomally which becomes transformed into an individual with an almost complete male organisation.

It is generally accepted that the agent responsible for the actual transformation of the gonads is the internal secretion of the testis—the male hormone. It may be assumed that the external factors which are primarily responsible for the reversal of sex act through the medium of the ductless glands.

Lillie found that twins of cattle are derived exclusively from

separate zygotes, so far as the evidence from sixty-one cases goes. The embryonic membrane of such twins, however, fuse in an early stage (embryos of about 30 mm.) and the blood-vessels of the two individuals anastomose. If one is male and the other female the reproductive system of the latter fails to develop its usual characters, and characters of the male appear instead to a variable extent which appears to depend upon variations in time and degree of the vascular anastomosis. Such individuals have long been known as free-martins. The gonad is testis-like in form and structure owing to complete suppression of the ovarian cortex and hypertrophy of the homologue of the seminiferous tubules. The Müllerian ducts usually degenerate, and the Wolffian ducts may develop into quite typical vasa efferentia; *gubernacula* arise as in the male; but, save in very exceptional cases, the external organs of reproduction and the mammary gland conform to the female type. In rare cases (about one in eight cases of two-sexed twins) the vascular anastomosis fails to develop, and in such cases the female is normal. No abnormalities of the reproductive system of the male arise in two-sexed twins.

Sex-determination in the zygotic sense is thus seen not to be the exclusive determiner of sex-differentiation in mammals, even in respect to the most fundamental sex-characteristics. The possibility of complete sexual inversion, by means of hormones of the opposite sex, and of control of sex-determination in this sense, is thus postulated.

Chapin who made a microscopic study of the reproductive system of foetal free-martins demonstrated that there is a fusion of the embryonic membranes and a subsequent anastomosis of blood vessels of the cattle twins. If one twin be male and one be female, the latter is commonly sterile. This is the result of the introduction of the interstitial secretion of the male into the blood of the female. It is manifested by the development toward the male condition, of those organs in the free-martin which are present in the indifferent stage (*rete*, first set of sex cords, primary *albuginea*), and the absence of those organs which develop in the normal female at sex differentiation or later (cords of Pflüger, definitive *albuginea*, union of Müllerian ducts to form uteruses).

There is much variation in the reproductive organs of the free-martins. This is due to two variable factors: (1) the time at which the interstitial secretion of the male embryo may first enter the circulation of the female embryo, and (2) the amount of secretion which may be introduced.

Willier who has more recently investigated the structure and homo-

logies of the gonads of the free-martin shows that in the free-martin (a sterile female co-twin to a normal male in cattle) an indifferent gonad with a primary female determination, under the influence of sex hormones from the male twin, may develop variable degrees of transformation in the male direction. So far as the structural evidence from sixteen cases (seven foetal and nine postnatal) goes, the reproductive glands of free-martins may be placed into three distinct groups, which may be characterized as low, medium and high degrees of transformation in the male direction, and constitute, therefore, a chain of connected links between an embryonic ovary and a testis. Every organ of these modified free-martin gonads is affected. The sexual chords exhibit a series of gradations between medullary cords and seminiferous tubules (complete except that male sex cells are lacking). The *rete ovarii* transforms into a *rete testis* chiefly by developing connections (*tubuli recti*) between the *rete* tubules and the epididymal tubules. In the least transformed gonads the epididymis is absent; in gonads exhibiting a moderate degree of transformation the head of the epididymis alone is present, and in the most completely transformed gonads a complete epididymis is developed. The distribution of the blood-vessels ranges from a typical ovarian to a typical male arrangement. It is thus seen that the most fundamental sex organ may be rather completely inverted by means of hormones of the opposite sex. Sex differentiation, then, is not exclusively determined by the union of the gametes.

But, as is illustrated in the cases of abnormality already described, the spermatie tissues may not become expressed until the ovarian have attained functional maturity and it has been shown that the appearance of a small amount of spermatie tissue upon the inner border of a gonad which previously has had every character of a normal ovary, is associated with the immediate degeneration of the ovarian tissues and a gradual but inevitable assumption on the part of the individual of the male organisation.

In these circumstances, if the gonad tissues exert their influence by means of internal secretions, then that of the testis must be more powerful by far than that of the ovary for the former wipes out the ovarian tissues and directs the imposition of male characters.

There is, in the frog, an antagonism of sex hormones and the ovarian is powerless in the presence of the spermatie. Quantity, apparently, is not a factor, for a very small nodule of testicular substance can still provide sufficient of the male hormone to wipe out the great mass of ovarian tissue and its abundant internal secretion.

A difficulty naturally arises. If the above be true, then there is reason to question the accepted statement that Bidder's organ is a rudimentary ovary. This organ persists in the male but disappears in the female, which suggests that it is spermatogenic rather than ovarian in nature, but so deficient in interstitial tissue that the hormone of the ovary, becoming exhibited in the absence of the hormone of the spermatogenic tissues, produces its ultimate destruction. In this connection, it will be remembered that Cerruti found spermatozoa actually within a Bidder's organ and that Hoffmann described rudimentary seminal tubules therein, whilst the experimental work of Harms supports the idea that Bidder's organ is male in nature.

Harms maintains that Bidder's organ is an organ of internal secretion and has conducted experiments which show that the development of the typical male finger-pads is controlled in some part by this organ, for, while extirpation of the testis or of Bidder's organ has no influence upon the development of the pads, yet if, after extirpation of both testes and Bidder's organs, a Bidder's organ is grafted in the dorsal lymph-sacs, the typical seasonal development of the pigmented pads follows in due course.

Goldschmidt has shown that Bidder's organ undergoes changes which are parallel to the sexual cycle and that in the case of the male there is increased activity and regeneration of its constituent cells, co-incident with the formation of the spermatozoa.

Cytologically it has not been proved that the cells which constitute Bidder's organ are ovarian, and there undoubtedly are reasons for questioning the generally accepted opinion that this organ is a rudimentary ovary.

SUMMARY.

1. It is shown that the recorded cases of abnormality of the reproductive system illustrate the process by which an individual, at one time possessing solely the complete sex-equipment of the female, comes to exhibit the organisation of the male. The sole female character which remains in what otherwise appears to be a typical male may be the full development of the Müllerian ducts, or the presence of ova amid the spermatogenic tissues.

2. Such a transformed individual not only has the male organisation but also behaves and functions as a male.

3. It so happened that a transformed individual, functioning as a male, fertilised the eggs of a normal female. This male was one of an

original population including 80 % males. All (774) of his offspring which attained a sufficient development to permit identification of the sex were females. Including these 774 females, the tadpoles produced from the original population were 23 % males and 77 % females.

4. This "swing-back" is taken as evidence which supports the conception that the frog has a chromosome constitution of the XY, XX type, and that these cases of abnormality are females (XX), the chromosome constitution of which has become over-ridden by external factors, and which are "somatic" males or masculinised females. These, being XX in chromosome-constitution, mating with normal females, also XX in constitution, will produce a generation consisting entirely of females. The presence of such "somatic" males in a population will thoroughly disturb the sex-ratio of the succeeding generation, producing a "swing-back" which is a certain indication of their presence and reproductive activities.

5. The mechanism by which the individual is thus transformed is one which acts through the internal secretions of the gonads. It is shown that in the frog the phenomenon of sex-reversal is very similar to the same process in cattle save that in the frog there is an antagonism of the sex-hormones and that the ovarian is powerless in the presence of the spermatie.

6. It is shown that there is a most intimate relation between the primary sex-glands and the accessory sexual apparatus and the secondary sexual characters.

7. Reasons are given for questioning the generally accepted opinion that Bidder's organ is a rudimentary ovary.

Since the present writer first offered a suggestion as to the possible significance of the abnormalities in frogs, an important contribution to the literature dealing with the subject of reversal of the sex-organisation has been made by CHAMPY, C. (*C. R. Acad. Sci. Paris*, Séance du 9 Mai, 1921.)

Champy had previously observed that the annual incidence of spermatogenesis in Tritons could be prevented by starvation, and that in males, killed in Spring after such treatment, the testicles had become replaced by fat which contained groups of undifferentiated gonocytes.

More recently he found that two such males when fed intensively began to assume the external characters of the female. One was killed for examination and the gonad was found to have been replaced by fat as in the previous cases. The other specimen was kept alive for further observation. Its history was known; it had been a perfect and complete male, and had fertilised the eggs of a normal female. Gradually it came to be exactly like a female in appearance. It was ultimately killed. On examination each testis was found to have been replaced by a wide

long strip of fat within which was an elongated organ with the appearance of an immature ovary and enclosing a typical oviduct. On histological examination the organ proved to be an ovary consisting mainly of young oocytes.

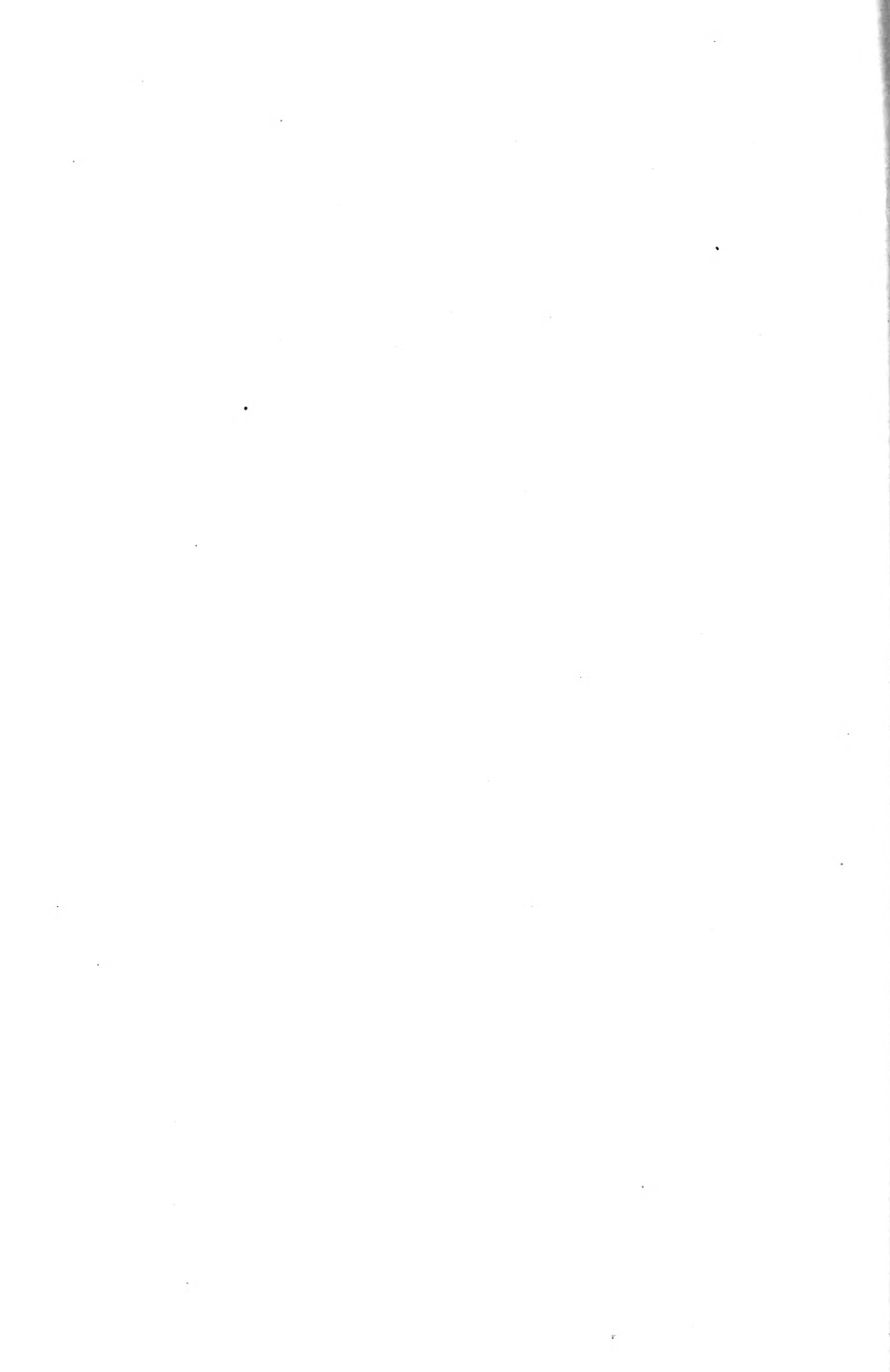
"Knowing the previous history of the animal there can be no doubt that we have here a case of complete sex-reversal."

Champany has not yet bred from such a feminised male.

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A STUDY OF THE SEGREGATION OF A QUANTITATIVE CHARACTER IN A CROSS BETWEEN A PURE LINE OF BEANS AND A MUTANT FROM IT.

BY I. LEITCH.

(With Four Text-figures.)

THE service which Mendel and his rediscoverers rendered to the study of heredity in demonstrating that certain qualitative characters behave, relatively to each other, as separate entities, has been paralleled by Professor Johannsen, Jennings and others for quantitative characters. Until their researches were made, size, for instance, was regarded in the light of Darwin's and Galton's work as something capable of endless variation—the net result, in any particular case, of a summation of causes, natural selection, fitness, and other equally indefinite concepts. What Professor Johannsen did was to delimit certain quantitative characters; to show that, although to some extent influenced by environment, still they are definite characters, capable of accurate description and analysis. What makes the problem of quantitative differences appear more difficult than that of differences in colour and other such qualities is that they cannot be described and classified on inspection, but the two problems approach in cases where, for instance, cumulative colour factors operate, and quantity of colour enters the field. There appears indeed to be no reason to regard the problems as essentially different.

Professor Johannsen established for quantitative characters the principle of working with homozygous, "pure," material as the basis of all analysis. He demonstrated for his pure lines of beans and barley that such material breeds true; that, in a homozygote, such characters as size and weight are as constant as greenness or smoothness; and he made familiar the exact description and comparison of such characters by means of their distribution curves. For instance, the sizes of the beans in two plants, or pure lines, or aggregates of beans, will be described fully and accurately in any given case by the distribution curves of their lengths and breadths, and the comparison of different sizes will be a question merely of the comparison of distribution curves. These curves have not

in the first place any mathematical or statistical end in view, but are only a summary expression of exact measurements, and become the equivalents of such descriptive terms as red and white or smooth and rough.

The constancy of quantitative characters having been shown, it remained to prove whether or not they behave in a cross like qualitative characters, showing the usual forms of Mendelian segregation. Crosses made between beans of different lengths and breadths showed segregation similar to that where several cumulative characters are in question, as Professor Johannsen points out in his *Elemente der exakten Erblichkeitslehre*, 2nd Ed. p. 558. And further he communicates interesting results in connection with the origin of the mutation dealt with in this paper and of another mutation. He finds that the latter mutation, occurring as a heterozygote, gives the original form and a new form as segregates in the simplest Mendelian ratio, 1 : 2 : 1. [*Elemente*, 2nd Ed. p. 653.]

The data to be dealt with in this paper are the results of a cross between the pure line *E* and a long mutant from it, made in hope of throwing some light on the nature of the mutation. I am indebted to Professor Johannsen for the following account of the origin of the material in question.

"The beans used were a variety of *Phaseolus vulgaris nana* called brown Princess beans, cultivated for commercial purposes in certain districts in Fyn. In 1901 a number of pure lines were isolated from bought material. Only biotypes were chosen of which the seeds did not touch each other in the pod, but developed quite freely. And all types where there was a tendency to abortion, that is, where the pods were not filled with seeds, were excluded. All the biotypes were therefore from the beginning, healthy, fertile and with well-formed seeds, suited to be measured singly with the apparatus described in the *Elemente der exakten Erblichkeitslehre*, 2nd Ed. p. 13.

"As to fertilisation, many years' work with the pure lines in question has shown that, when the beans are cultivated under a volière of wire netting with a mesh of about 2 cms. there is little chance of crossing. And all the experiments made on these pure lines have clearly shown their genotypical constancy; all selection has been without result. Further, in the crosses that have been made—and made only with great difficulty—it has appeared at once that the conditions, as regards inheritance and variation, are quite different from the behaviour of pure lines, as is pointed out in the Report of the Third International Con-

ference in Genetics, (1906), p. 98, and as is demonstrated in the *Elemente*, 2nd Ed. p. 558.

"The pure line *E*, with which the present paper is alone concerned, is distinguished from all others in my material by having pure white petals and a yellow-white colour in the rest of the flower, without a trace of violet. The other lines of Princess beans have a violet tinge, often weak but unmistakable. And in the crosses made between *E* and other lines, the F_1 generation has always had this violet colour in the flower, and the F_2 generation has split strongly and clearly giving plants with violet and plants with white flowers in the ratio 3:1.

"Therefore line *E* is exceedingly well suited for further studies where it is important to be sure that no inadvertant cross has occurred; such a cross would at once appear in the colour of the flowers. Line *E* then, as I have described in my paper 'Om nogle Mutationer i rene Liniers' (*Biol. Arbejder tilegnede Eug. Warming*, K benhavn, 1911), has twice shown a sudden change in genotypical constitution, 'mu(c)tation'—and that without any alteration in its white colour—and one of the new biotypes, which from its appearance (probably by vegetative mutation) was homozygous and as such had proved constant for a number of years, was chosen to test further the nature of the mutation. A cross was made between the original, unaltered, *E* type and the mutant in question, mutant \times original. The immediate result of the cross was three seeds which were sown and gave in all 62 descendant seeds, which have thus F_2 embryos in F_1 seed-coats."

Of these 62 seeds, two were rejected as misformed and the remaining 60 sown in six rows of 10 each, with two control rows of *E* and *M* respectively. It was the harvest from these 60 beans that was handed over to me in the Autumn of 1914 for analysis.

The following figures from Professor Johannsen's paper show the amount of the difference between the original pure line *E* and the long mutant, which, for convenience, we call *M*.

Original type	...	<i>L</i> 12.459	<i>B</i> 9.017	<i>I</i> 72.4
Long mutant	...	<i>L</i> 13.564	<i>B</i> 9.137	<i>I</i> 67.4

(*I* is the length-breadth index, $100 B \div L$).

Or comparing the indices through a number of years,

Year	Original type	Long mutant	Difference
1906	72.4	67.4	5.0
1907	77.8	71.2	6.6
1908	72.4	66.8	5.6
1909	75.3	69.5	5.8
1910	73.3	67.1	6.2
1914	68.6	65.0	3.6
1917	69.2	64.3	4.9

With regard to the general conditions under which the further experiments were conducted, in 1914, 1915 and 1916 the beans were grown in the volière in the experimental part of the Botanical Garden. The year 1916 was in every way unfortunate. The weather was bad and the ground "bean-tired." The results for 1916 are therefore not as good as for the other years. For that reason, the beans were sown in 1917 and 1918 outside the volière in the experimental garden. The ground in which the beans were planted was, as far as possible, uniform, and they were planted exactly equidistant from each other. More or less room to grow has considerable influence on the size and number of the beans produced by a plant, and to avoid disturbances from that cause, any gaps occurring from failure to germinate were filled with beans from another pure line with violet pigment in the flowers and stems and black seeds of a different shape. No trace of cross-fertilisation ever appeared in either race, inside or outside the volière.

The beans are sown in May and ripen about the end of August, and after harvesting are spread out to dry in a loft. They must not be dried too quickly nor subjected to much warmth or the pods will open and much material be lost. When the beans are thought to be dry, weighing tests are made, a sample fresh from the pods being weighed, left for a few days in a warm room and again weighed. When the weight is constant all the beans are removed from the pods, plant by plant, and carefully examined. Any that may be unripe, all misshapen beans and all that are spotted with fungi, though only to the extent of slight discoloration, are rejected. The reasons for the rejection of these first two classes of seed are obvious. Beans that are unripe or misshapen will give measurements that are abnormal and incorrect. But neither unripe nor misformed beans are numerous, and misformed ones occur usually together in pods that have been curved in growth by some accident of position or by injury. The most serious ground of rejection lies in the attacks of fungi and seeds so injured must be rejected for two reasons. In the first place, it cannot with certainty be said that the fungus is without influence on the size of the bean, and, in the second place, not only are such beans useless as seed themselves, but they are liable to infect others stored in the same glass.

Each year the original pure line and the mutant were sown as controls, and in 1916, 1917 and 1918, when the number of rows had become big, ten rows of controls were sown in all, five of *E* and five of *M*, distributed, one of each together, at equal distances over the field. The variation in the controls will give a picture of the differences due to inequalities in the ground.

In measuring the beans both length and breadth were recorded. But, as far as the problem in hand is concerned, the length is of most importance. The range of difference being greater, it is obviously easier to distinguish differences in length than in breadth. Therefore, in the data accompanying this paper, only curves for length are included. Further, since after 1914 it was impossible to continue measuring every bean, a random sample of 25 beans was measured from each plant.

In the analysis of the material two different methods of representation were employed. The first was the plotting of the distribution curves for the lengths and breadths of the beans of each row of plants. Except in 1914 each row contains plants from the seed of one parent plant only. The curve of a row in 1915 will therefore be an expression of the genotypical nature of the plant from which its seed was selected. And so for each year. The curves for the six rows in 1914 are not so distinguished, and from them only general deductions can be drawn as to the general nature of the 60 seeds sown. These curves of distribution were plotted directly and not calculated to constant area; for, plotted directly, characteristic differences are more striking, such as the flatter form of typical *M* curves and the typically lower fertility of the *M* type.

This method affords little help in the selection of plants for further breeding. For that purpose some method that would give a comprehensive graphic survey of the material is desirable, and is found in the plotting of what I call charts. On these charts length and index ($100L/B$) were plotted, the x axis giving length and the y index, and each plant being represented by a point whose co-ordinates were respectively the average length and index of its beans. Such a chart was made each year for the control plants of *E* and *M* on ordinary mm. paper. Over it the limits of their distributions were sketched on transparent mm. paper and the hybrid forms plotted there. This gives an immediate picture of the position of every single hybrid plant in relation to the two parent lines and the forms can be classified on inspection. The method is of course cumbrous and ill-suited for reproduction, but it proved of greater practical value than any other.

As to the 1914 harvest then, the 60 hybrid plants, bearing seeds containing F_2 embryos in F_1 seed-coats, show in their distribution curves a range of variation from below the lowest limits of the line *E* to the upper limit of *M*. And this fact at once suggests a complication of the problem. A distribution varying from the lowest limit of *E* to the upper limit of *M* might have been expected in accordance with what Professor Johansen found in the hybridisation experiments already referred to.

But it must be noted that to give such *transgressive* distributions there must be a *positive* difference in genotypical constitution between *E* and *M*. Of course it could not be said at this early date that these indications were reliable, but at least the indications were there and the problem had become enriched by the question of the cause of the transgressive variation.

The chart of the hybrids bore out and emphasised the evidence of the distribution curves, for here the measurements do not merge as they do in the curve for a whole row, but individual differences between the plants stand out. Some of the plants with the smallest beans lay quite outside the lowest limits of the *E* biotype, and there was an absence of forms intermediate between *E* and *M*, those which one would have expected to be most numerous. In selecting seeds from the hybrids for sowing in 1915, beans were chosen which, from their position on the chart, relatively to the chart of *E* and *M*, seemed likely to prove either segregated *E* forms or segregated *M* forms; in addition, two of the strikingly small lots and one which, alone, seemed to occupy a satisfactory intermediate position between *E* and *M*. These will be found in the first genealogical table (p. 202) marked, in 1914, with letters indicating the forms to which they were thought to belong; in all, six apparently *M*, two extremely short, the one intermediate just mentioned and the rest apparently typical *E*.

The harvest from these beans was as before gathered and preserved plant by plant, and a sample of 25 beans taken at random from each measured. The result was that in the six rows of plants whose seed had been selected as *M*, the beans of each plant belonged to that type; in the two rows whose seed had been selected as extremely short, all the plants bore seed whose distribution curves lay well to the left of the control curves for *E*. On the charts, the *M* seed gave only *M* beans in every case; the extremely short gave only forms lying in a group to the left of and higher than the *E* group. On the other hand, the distribution curves for the plants from the *E* seed showed the same transgressive variation as the 1914 curves; on the charts the plant averages stood out sharply and clearly as segregates, some belonging to the extremely short type, which we shall henceforth call *X*, some apparently *E* and some *M*.

The distribution curve for the intermediate—seed from plant 46, i, in 1914; row 9 in 1915—maintained its position, and on its chart the group of plants lay intermediate between the *E* and *M* groups without any evidence of segregation such as appeared in the groups last mentioned.

Thus a new type, *X*, shorter and broader than the original *E* type has been established; the segregated *M* remains constant and the apparent *E* seed gives plants bearing seed which is, plant by plant, either *X* or *E* or *M*. Taking these segregating rows alone, seven rows in all, and counting on the charts what forms are *M* and what are either *E* or *X*, the rows give respectively, 13 (*E* or *X*) and 9 (*M*): 17 (*E* or *X*) and 5 (*M*): 17 (*E* or *X*) and 7 (*M*): 18 (*E* or *X*) and 2 (*M*): 15 (*E* or *X*) and 7 (*M*): 16 (*E* or *X*) and 5 (*M*): and 16 (*E* or *X*) and 3 (*M*); in all, 112 non-*M* and 38 *M*, which is an ideal 3:1 ratio. At first no significance was attached to this ratio. In view of the intermediate between *E* and *M*, row 9 in 1915, and of the new *X* type, it was to be expected that *M* would also produce new extreme types.

To throw light on the questions which now arise the following selection was made for further breeding; two *M* types, the intermediate, and four of the segregating types. The rows chosen were rows 12, 5, 14 and 21 (segregating), 9 (intermediate) and 18 and [20, 22] (*M*), and these numbers have since been used to indicate the seven groups of descendants. The following summary account of the further experiments in each of the seven groups will be most easily understood if reference is made while reading to the genealogical tables on pp. 202—4.

As group 21 offers no complication of any kind it is a suitable starting-point. For sowing in 1916 were selected four of the extremely short types, two apparently *E* and two supposed *M*. The short were planted in rows 53, 48, 41 and 7 in 1916; the *E* seed in rows 12 and 17 and the *M* seed in rows 34 and 22. From the distribution curves for these rows it appears that the small types remain constant in position relatively to the control curves from the original lines; that the plants from the *M* seed bear beans true to the *M* controls; and, on the chart, the two apparent *E* types give some plants with *X* beans, some with *E* and some with *M*. With regard to the short *X* type there might possibly be a question as to whether row 7 is identical with the three rows 53, 48 and 41. It might be supposed that 7 was an intermediate between *X* and *E*. To test the point three short variates and one long were selected from 7 and planted in rows 63 (long) and 64, 65 and 66 (short), in 1917. The curves for these four rows are practically identical and it is certain that no segregation takes place. Further selection of plus and minus variates in 1918 also failed to show any difference. That is to say, to judge from group 21, the *X* type shorter and broader than *E*, once isolated, is fixed and constant.

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To test further the constancy of the *M* segregated types the longest four and the shortest (*I*) plant from row 22 were used as seed again in 1918 giving rows 46, 47, 48, 55 and 56. It will be seen that these give identical curves corresponding in type to the control curves for *M* in 1918. Further the two groups 18 and [20, 22], sown in duplicate from the seed of one plant in 1914, were continued in 1916, and row 20 from group 18 in 1918. It will appear also from their curves that their seed corresponds with the control *M* types and with the *Ms* segregated from group 21.

Group 12 behaves in a similar manner. In 1915 three *M* types, two extremely short, three apparent *Es* and one doubtful were selected for seed. In 1916 the *Ms* bred true, the *Xs* bred true and the apparent *Es* and the doubtful type split. Of particular interest in this group are the curves for rows 23, 24, 25, 26, 27 and 28 in 1918, representing selected short (23, 24, 25) and long (26, 27, 28) variates from an *X* group in 1916. The curves are identical, indicating again that the *X* type is homozygous and that therefore selection has no effect in altering the type.

Row 10 (1916) appeared of a rather doubtful composition. Although in general *M* in type, there were two doubtful, possibly intermediate plants, and one which produced certainly very few beans, but these so short that the possibility at least of something unusual had to be admitted. These were therefore sown; rows 9 (ext. short) and 13 and 14 (intermediate), with two of the longest types from row 10, rows 10 and 11. The curves show no difference of significance; the difference between 13 and 14, which seems the greatest, is in any case not greater than that between 68 and 18 of the control pure *Ms*.

In groups 5 and 14 occurred the only serious disturbance that arose, in that types selected as *X* did not in every case prove to be *X*. In view of the subsequent behaviour of their descendants they must, however, be regarded as very aberrant members of the intermediate heterozygous group usually selected as apparent *Es*. There is always transgressive variation, and 1916 was a very bad year. It will appear that other types too suffered, the beans being shorter than usual; and as the chief cause was, no doubt, that the ground was "bean-tired," the shifting of the types to the left had probably begun in 1915.

In group 5, then, there were selected in 1915 four supposed *X* plants, four *E* and two intermediates. In 1916 only one of the rows from supposed *X* seed bred true. The other three and the four *Es* showed segregation, while the two intermediate proved to be *M*. It is signi-

ficant that the intermediates in this case proved to be *M*, indicating that the same disturbance is operating here.

In 1917 the extremes from row 3 were sown, and as they give a typical example of the method of segregation, the chart of these plants has been chosen to illustrate the method. The curves for row 3 and other typical forms are also given. The constant *X*, row 45, was continued in the four rows 27, 28, 29 and 30 in 1917, and as 28 and 30 showed each one plant with beans of unusual length these two plants, with two short variates, were continued in 1918. The curves for these, 31, 33 (short) and 32, 34 (long), show at once that the aberration was without significance and that here again the *X* line breeds true.

The other rows segregate as before, giving *X*, *M* and a type that again splits.

In group 14 a similar disturbance appears in that, of the two apparently *X* types chosen as seed in 1915, one bred true and the other proved to belong to the segregating type. One *E* type chosen proved as before heterozygous. Three doubtful intermediate types were selected, and, of these, two, as in group 5, proved to be *M* while the third proved to be entirely different. It gave rise to a group of plants occupying a position similar to that of the parent plant, and like the 9 group already mentioned intermediate between *E* and *M*. Continued in 1917 this intermediate group, 6, shows a more scattered distribution but little or no evidence of segregation. To test the point, the extreme short variates (2) and longest (1) in row 37 were chosen as seed, the shortest and longest, at the same time unusually narrow, from row 39 and the two longest from 35. The two short 37s give rows 35 and 36 respectively in 1918 and the long variate, row 57. Both chart and curves show that there is no difference between them; indeed the curve of lengths for 57 lies, if anything, slightly to the left of those for 35 and 36. As regards the two rows selected from 39, 18 (the aberrant type) and 37 (the short), there is admittedly a slight difference. But the range of 18 is characteristic for the more diffuse types in this group, and 37 corresponds closely to the other rows just dealt with. 18 shows no trace whatever of the unusual breadth of its parent seed in 1917. It must therefore be concluded that there is no evidence of segregation in this group. Group 6 belongs to a non-segregating type intermediate between the original lines *E* and *M*.

The same behaviour is found throughout the group 9. From the 1915 material were chosen seven plants for seed, including those with the shortest and the longest seed. The general result was a group,

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somewhat diffuse, but still intermediate between *E* and *M*. For further analysis were chosen two very short types, one from row 9, the other from row 36; two very long types from row 31, and a number of typical forms between these limits, in all 18 rows. The two shortest types gave rows 49 (from 9) and 62 (from 36) in 1917; the two longest, rows 56 and 57. In 1917 rows 49, 56 and 57 are indistinguishable and the group of descendants is in this case very strikingly homogeneous and again intermediate between *E* and *M*. To this there is however one exception. The other of the very short forms, row 62, gives an isolated, very short, group immediately distinguishable from the intermediate group itself, and at once suggesting an *X* group. Continued in 1918 the 62 group, of which the three shortest and one longest plants were sown, proved as expected to give an *X* group, identical with the *X* forms segregated from other groups. Three extremely long types were also continued in view of the possibility of segregation taking place in that direction also. The result was, as before, negative.

Thus, this group, with the exception of the one case in which an *X* group is segregated out, behaves like the 6 group, remaining intermediate between *E* and *M*. It seems legitimate to assume that the *X* was produced by splitting in the same way as was found typical in the other groups; and so, to sum up the results, the hybrids between *E* and *M* either split into *M*, an entirely new type shorter and broader than *E*, and an intermediate type that again splits; or they do not split at all. The non-segregating type arises twice, independently, and in different years.

As to the significance of these results, first it is evident that the theory that mutations are due to the loss of a factor or factors cannot be applied here. From the moment the *X* type is established, the theory of loss of factors is insufficient. No system of recombination of factors, cumulative or otherwise, could explain the appearance of a new type lying outside the limits of the original forms. It is necessary to regard the difference between *E* and *M*, not as a case of presence and absence of a factor or factors, but as a case of positive difference. This does not necessitate the assumption that anything has been added. The simplest view seems to be that a factor has been modified in the original pure line, to give the mutation. Why not more than one factor? Because the fact that, as already indicated, the typical splitting into *X*, intermediates, and *M*, gives a ratio of non-*M*s to *M*s of 3:1, a result confirmed in 1916 when the total number of rows splitting was 13, giving a total of 176 non-*M* plants; 63 *M*s points to there being

only one change. That, together with the failure of selection to show any further splitting in the *X* or *M* group, seems a sufficient indication that only one factor has been altered in *E* to produce the mutation *M*.

However, this modification must not be taken in any restricted sense. There is every reason to interpret the change in the broadest fashion. In the first place, as will be evident from the curves of distribution, and as is strikingly evident in handling the material, the *M* type produces usually fewer beans than the original *E* type or the *X* type. But there is certainly a correlation between the number of beans produced by a plant and their size, and whether the difference between the types be regarded as a difference in size or in fertility, primarily, is worth considering, though the point may not be of great importance. Further the *M* type is much more liable to be attacked by fungus than the *E* and *X* types. No attempt has been made to determine the reason for this, but it indicates that the change from *E* to *M* must be regarded as a change in the reaction of the whole organism.

If the change from *E* to *M* could be regarded as a sudden discrete transformation of one factor into a modification functioning as a new factor, the hybrids between *E* and *M* would be doubly heterozygous and they would be expected to split into a variety of types including some such type as *X* and possibly a type still longer than *M*. If the factor altered be called *A* and it be considered as modified to *B*, then the hybrids would have the composition *AaBb*, and to explain what really does happen, it would be necessary to postulate complete coupling between *A* and *B*. In addition it would be necessary to assume that forms containing neither factor are indistinguishable from *aaBB* (the *M* form); the *X* form then would be the double homozygote with both factors; or alternately, if presence of factors be taken to mean additional size, and *B* be regarded as modified into *A*, it must be assumed that *AABB* is indistinguishable from *AAbb*. And even so, the difference between the two heterozygous forms, one of which is phenotypically like *E* and the other intermediate between *E* and *M*, remains to be accounted for. This may prove to be a very far-fetched attempt to reconcile the results with Mendelian results in general and until other work on similar material has thrown more light on the subject, it is not a very profitable discussion. The one point stands out, that the theory of loss of factors here fails to account for the nature of the mutation.

With regard to the difference between the behaviour of the groups of heterozygous plants in general and the two aberrant, similar groups 6 and 9, Professor Johannsen has suggested the possibility of cytological

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difference, and efforts will be made to have the types examined by an expert. Where there is anything unexplained there is always hope of fresh discoveries.

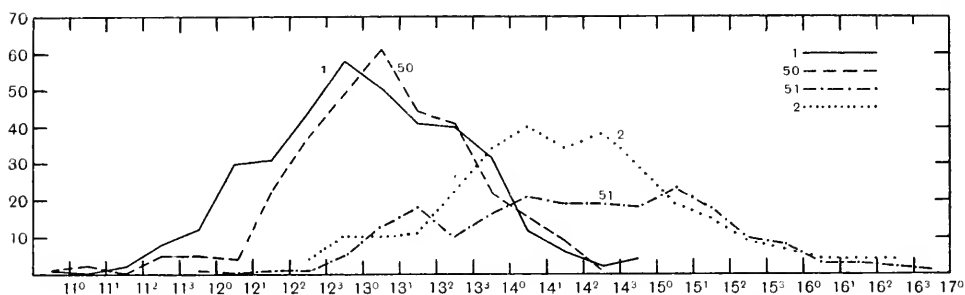


Fig. 1. Typical Control Curves, 1917. 1 and 50 : *E*. 2 and 51 : *M*.

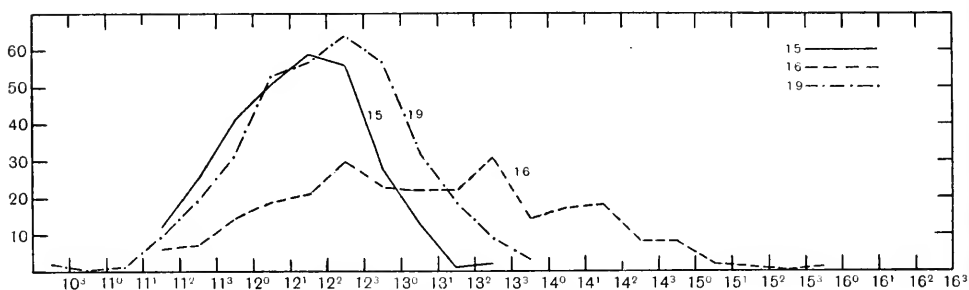


Fig. 3. Group 5 (1917). Segregates from 3 (1916).

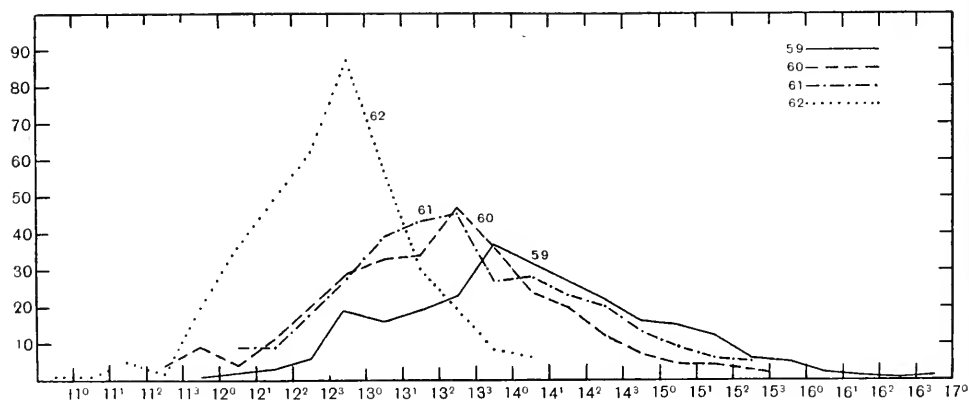


Fig. 4. Group 9 (1917). Segregates from 66 (1916).



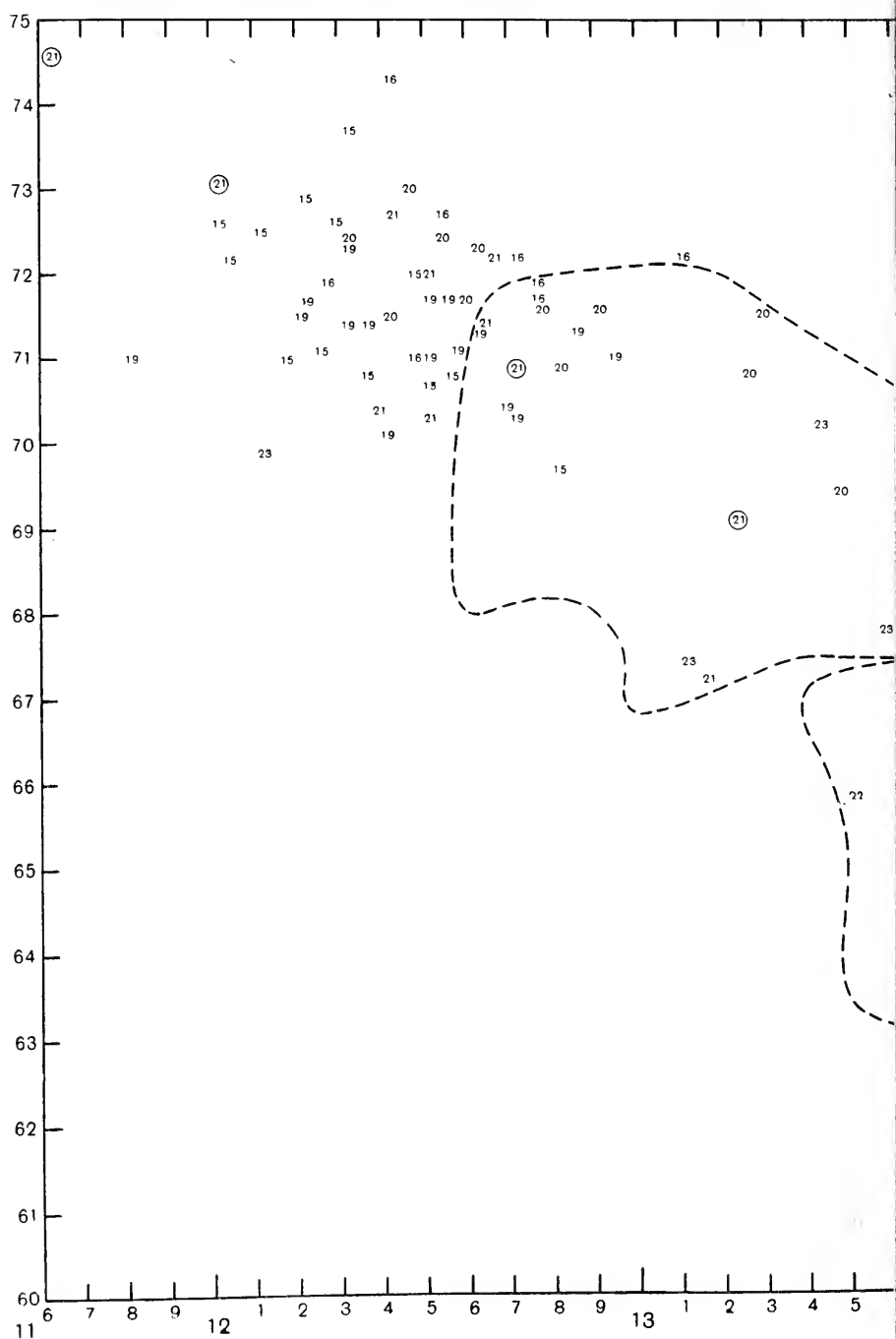
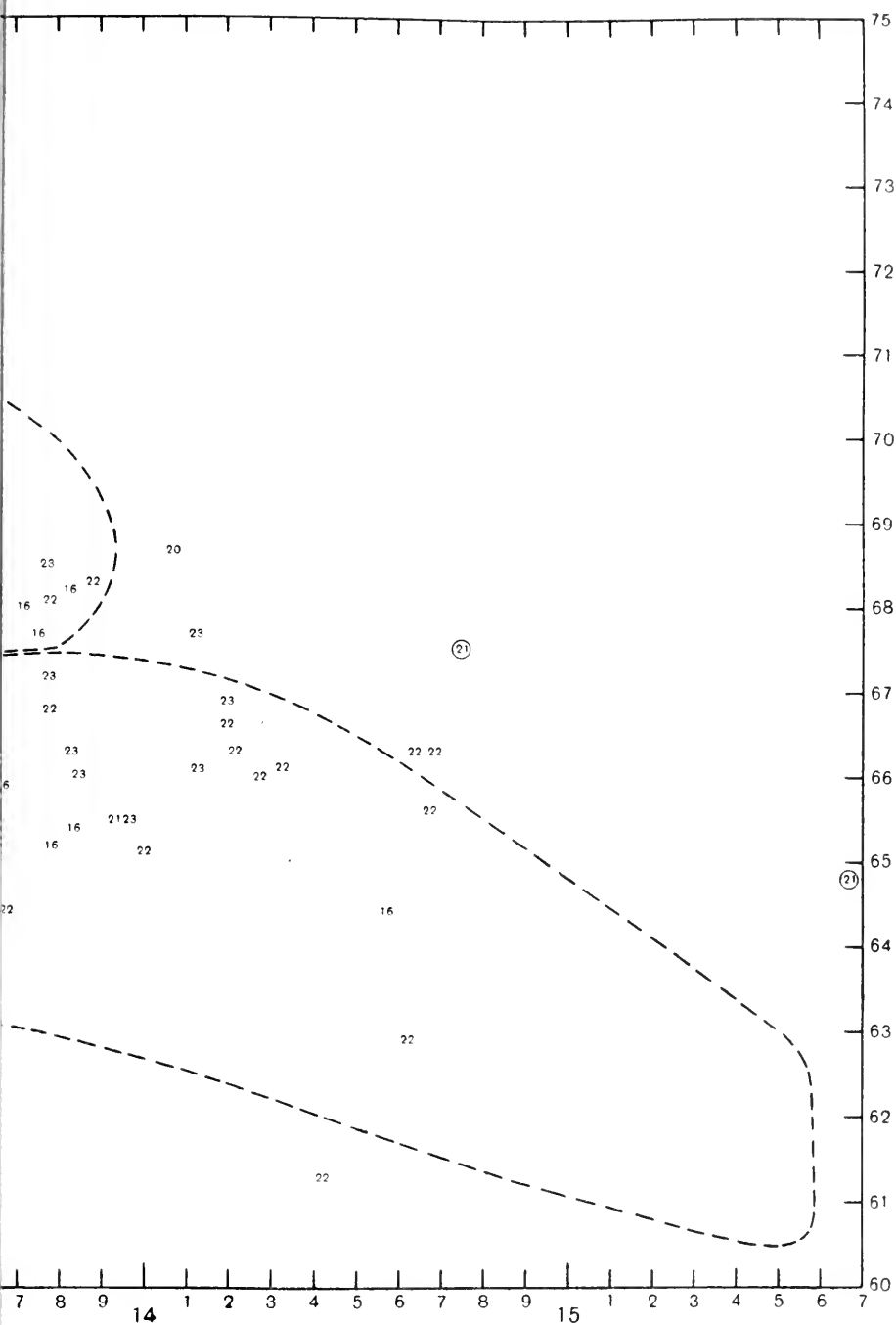


Fig. 2. Rows 15, 16, 19, 20, 21, 22, 23 in 1917.

Dotted lines give limits of distributions of controls *E* and *M*.

The *x*-axis gives length : the *y*-axis index = 100 length/breadth.



The numbers refer to rows and each number represents a plant.
Circles indicate that these plants were selected for sowing in 1918.

No. of row	9 ²	9 ³	10 ⁰	10 ¹	10 ²	10 ³	11 ⁰	11 ¹	11 ²	11 ³	12 ⁰	12 ¹	12 ²	12 ³	13 ⁰	13 ¹	13 ²	13 ³	14 ⁰	14 ¹	14 ²	14 ³	15 ⁰	15 ¹	15 ²	15 ³	16 ⁰	16 ¹	16 ²	16 ³	17 ⁰	17 ¹	17 ²		
1915	11	—	—	—	—	—	3	4	6	12	7	29	33	46	41	34	39	48	46	31	27	16	8	2	3	1	—	—	—	—	—	—	—	—	
23	—	—	—	—	—	—	—	—	1	4	10	23	20	20	30	21	31	22	32	20	26	12	12	8	—	2	—	—	—	—	—	—	—	—	—
1916	1	—	—	—	—	—	1	1	8	3	5	6	3	10	6	19	12	16	10	8	2	1	—	1	—	—	—	—	—	—	—	—	—	—	—
14	—	—	—	—	—	—	4	1	6	4	12	14	27	32	44	41	39	42	45	31	19	10	13	3	—	—	—	—	—	—	—	—	—	—	—
28	—	—	—	—	—	1	—	1	1	9	3	15	19	19	48	45	53	69	48	46	29	18	10	5	1	2	—	—	—	—	—	—	—	—	—
42	—	—	—	—	—	—	—	—	1	10	8	15	20	28	29	39	28	30	20	16	5	4	—	—	—	—	—	—	—	—	—	—	—	—	—
55	—	—	—	—	—	—	—	—	1	9	5	6	12	15	30	20	15	12	10	8	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1917	2	—	—	—	—	—	—	—	—	—	—	—	—	4	10	10	11	22	34	40	34	38	29	19	15	9	7	4	4	4	—	—	—	—	
18	—	—	—	—	—	—	—	—	—	—	—	—	—	3	3	4	3	6	3	5	6	18	9	17	16	3	6	5	2	—	—	3	—	—	
33	—	—	—	—	—	—	—	—	—	—	—	2	4	5	12	16	14	19	15	23	22	18	17	12	8	3	1	1	—	—	—	—	—	—	
51	—	—	—	—	—	—	—	—	—	1	—	1	1	5	13	18	10	16	21	19	19	18	23	18	10	8	3	3	2	1	—	—	—	—	
68	—	—	—	—	—	—	—	—	—	1	—	4	5	8	16	29	23	36	35	26	28	14	13	2	7	1	2	—	—	—	—	—	—	—	
1918	2	—	—	—	—	—	2	2	3	4	10	14	19	28	32	41	38	32	37	28	16	7	3	1	1	1	—	—	—	—	—	—	—	—	
16	—	—	—	—	—	—	—	—	—	4	4	9	9	16	29	34	36	34	39	34	19	17	6	5	3	2	—	—	—	—	—	—	—	—	—
30	—	—	—	—	—	—	2	—	—	3	3	8	22	22	24	32	37	32	28	19	12	4	4	2	1	—	1	—	—	—	—	—	—	—	
43	—	—	—	—	—	—	—	—	—	1	2	3	6	9	25	40	34	35	48	29	20	22	13	10	9	3	1	—	—	—	—	—	—	—	—
64	—	—	—	—	—	—	—	—	1	4	1	4	13	15	26	30	36	43	36	34	24	9	11	6	6	1	1	1	—	—	—	—	—	—	—

Journ. of Gen. xi

Journ. of Gen. et

Curves of Lengths of Controls : Original : 1915—18.

No. of			Orbits of <i>Longus</i> of <i>Comoros</i> : <i>Origitae</i> , 1919—1920.																															
Year	row		9 ²	9 ³	10 ⁰	10 ¹	10 ²	10 ³	11 ⁰	11 ¹	11 ²	11 ³	12 ⁰	12 ¹	12 ²	12 ³	13 ⁰	13 ¹	13 ²	13 ³	14 ⁰	14 ¹	14 ²	14 ³	15 ⁰	15 ¹	15 ²	16 ⁰	16 ¹	16 ²	17 ⁰	17 ¹	17 ²	
1915	2	—	—	—	1	6	5	2	4	13	21	35	55	77	115	104	73	45	19	9	1	—	—	—	—	—	—	—	—	—	—	—	—	—
1916	2	—	—	—	—	1	4	7	9	19	30	34	55	39	26	19	7	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
15	—	—	—	—	—	1	1	2	6	8	18	20	39	56	76	85	51	29	13	4	—	1	—	—	—	—	—	—	—	—	—	—	—	—
29	—	—	—	—	—	—	—	1	3	4	9	12	20	25	36	69	81	62	62	19	8	2	—	—	—	—	—	—	—	—	—	—	—	—
43	—	—	—	—	—	—	—	3	1	7	3	15	14	40	41	46	28	38	8	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—
56	—	—	—	—	—	—	—	6	1	7	6	11	17	23	27	23	18	14	4	7	2	1	—	—	—	—	—	—	—	—	—	—	—	—
1917	1	—	—	—	—	—	—	1	—	2	8	12	30	31	44	58	51	41	40	32	12	6	2	4	—	—	—	—	—	—	—	—	—	—
17	—	—	—	—	—	—	—	—	1	2	1	2	9	15	25	33	32	33	15	14	7	2	—	—	—	—	—	—	—	—	—	—	—	—
32	—	—	—	—	—	—	—	—	—	1	—	2	4	10	17	14	22	40	33	43	37	18	17	4	1	1	—	—	—	—	—	—	—	—
50	—	—	—	—	—	—	—	1	2	—	5	5	4	22	37	49	61	41	22	15	9	1	—	—	—	—	—	—	—	—	—	—	—	—
67	—	—	—	—	—	—	—	—	1	1	2	2	3	10	28	34	46	46	38	27	18	10	5	—	1	—	—	—	—	—	—	—	—	—
1918	1	—	—	—	—	—	—	1	3	7	19	22	23	27	44	31	27	21	12	8	3	—	—	—	—	—	—	—	—	—	—	—	—	—
15	—	—	—	—	—	—	—	2	5	9	12	30	34	38	58	40	41	33	13	15	8	3	—	—	2	—	—	—	—	—	—	—	—	—
29	—	—	—	—	—	—	—	3	8	14	16	30	29	32	25	28	26	22	14	10	2	4	—	—	2	1	—	—	—	—	—	—	—	—
42	—	—	—	—	—	—	—	4	5	4	9	10	24	31	46	56	40	38	12	9	15	4	—	—	—	—	—	—	—	—	—	—	—	—
63	—	—	—	—	—	—	—	—	1	2	2	11	19	15	20	36	37	45	36	38	32	13	12	6	1	1	—	—	—	—	—	—	—	—

13

Curves of Lengths, 1914.

No. of row	92	93	10 ⁰	10 ¹	10 ²	10 ³	11 ⁰	11 ¹	11 ²	11 ³	12 ⁰	12 ¹	12 ²	12 ³	13 ⁰	13 ¹	13 ²	13 ³	14 ⁰	14 ¹	14 ²	14 ³	15 ⁰	15 ¹	15 ²	15 ³	16 ⁰	16 ¹	16 ²	16 ³	17 ⁰	17 ¹	17 ²	Type
41	—	—	—	—	2	1	4	6	14	34	57	87	120	130	134	55	42	11	5	2	1	—	—	—	—	—	—	—	—	—	—	—	Control original	
42	—	—	1	—	1	1	1	6	10	31	58	88	146	155	117	81	43	17	9	2	2	—	—	—	—	—	—	—	—	—	—	—	Control mutant	
39	—	—	—	—	—	—	2	5	9	16	9	24	58	75	106	120	106	88	47	39	21	22	13	2	1	1	—	—	—	—	—	—	Control mutant	
40	—	—	—	—	—	—	1	—	1	3	4	7	13	19	22	50	47	85	76	91	70	54	50	21	10	5	1	—	—	—	—	—	—	Hybrid
43	—	—	—	—	—	1	3	11	15	32	49	66	74	81	62	59	55	39	25	22	10	7	3	1	1	—	—	—	—	—	—	—	Hybrid	
44	—	—	—	—	3	2	5	10	18	33	59	80	78	50	59	80	54	50	30	22	10	6	4	2	1	—	—	—	—	—	—	—	—	Hybrid
45	—	—	—	—	3	4	8	16	30	37	50	52	64	79	72	55	39	41	20	18	7	—	—	3	—	—	—	—	—	—	—	—	—	Hybrid
46	—	—	—	—	—	—	1	2	11	21	40	56	67	89	72	73	68	59	37	19	26	9	5	2	1	—	—	—	—	—	—	—	Hybrid	
47	—	—	—	—	—	—	3	—	4	11	17	46	52	72	86	96	88	71	69	37	33	20	10	6	4	1	—	—	—	—	—	—	—	Hybrid
48	—	1	—	—	2	4	19	32	79	116	129	122	121	114	84	64	35	34	20	8	8	2	2	—	—	—	—	—	—	—	—	—	—	Hybrid

Curves of Lengths, 1915.

No. of Year	row	92	93	10 ⁰	10 ¹	10 ²	10 ³	11 ⁰	11 ¹	11 ²	11 ³	12 ⁰	12 ¹	12 ²	12 ³	13 ⁰	13 ¹	13 ²	13 ³	14 ⁰	14 ¹	14 ²	14 ³	15 ⁰	15 ¹	15 ²	15 ³	16 ⁰	16 ¹	16 ²	16 ³	17 ⁰	17 ¹	17 ²
1915	3	—	—	—	—	2	1	3	11	11	24	27	30	43	39	35	44	41	53	37	36	26	15	6	3	4	—	—	—	—	—	—	—	—
	7	—	—	—	1	6	11	11	25	32	40	51	38	52	39	37	29	26	39	18	15	13	9	2	1	1	—	—	—	—	—	—	—	—
	4	—	3	2	7	3	11	22	41	73	82	99	74	73	31	9	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	15	—	—	—	—	—	2	—	5	5	8	13	25	27	45	52	49	41	62	46	31	23	8	7	5	5	1	1	—	—	—	—	—	—
	19	—	—	—	—	—	—	—	—	10	9	11	30	35	34	38	58	52	73	51	40	22	18	5	3	—	—	—	—	—	—	—	—	—
	6	2	3	5	10	10	19	25	52	72	104	103	100	69	30	6	1	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	8	1	2	8	11	10	23	18	46	69	74	62	58	44	27	21	23	11	7	6	6	—	—	—	—	—	—	—	—	—	—	—	—	—
	10	—	—	—	—	—	1	1	5	10	15	14	23	29	42	34	42	36	55	36	36	21	13	10	5	1	3	2	—	—	—	—	—	—
	16	—	—	—	—	—	—	3	9	12	22	25	31	41	39	44	42	44	28	21	11	14	10	5	—	—	—	—	—	—	—	—	—	—
	12	—	1	3	1	8	16	21	25	24	55	61	74	68	53	31	29	28	25	11	6	6	2	2	2	—	—	—	—	—	—	—	—	—
	14	—	—	—	—	—	—	—	—	17	22	40	62	49	52	53	45	27	32	26	11	12	3	4	—	—	1	—	—	—	—	—	—	—
	9	—	—	—	—	—	4	7	10	23	39	50	63	49	50	46	40	31	33	21	16	5	3	1	—	—	—	—	—	—	—	—	—	—
	17	—	—	3	3	2	4	7	22	35	47	71	61	60	54	43	25	22	14	14	12	4	4	—	—	—	—	—	—	—	—	—	—	—
	21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	18	—	—	—	—	—	—	—	—	3	1	4	3	10	13	22	32	34	49	48	39	33	25	25	15	5	4	—	—	—	—	—	—	—
	20	—	—	—	—	—	—	—	—	5	5	8	13	24	26	33	30	37	35	42	29	35	28	12	7	3	1	2	—	—	—	—	—	—
	22	—	—	—	—	—	—	—	—	4	6	14	11	19	26	34	37	32	43	38	40	39	36	25	13	4	4	—	—	—	—	—	—	—

Curves of Lengths of Group 21.

No. of Year row	9 ²	9 ³	10 ⁰	10 ¹	10 ²	10 ³	11 ⁰	11 ¹	11 ²	11 ³	12 ⁰	12 ¹	12 ²	12 ³	13 ⁰	13 ¹	13 ²	13 ³	14 ⁰	14 ¹	14 ²	14 ³	15 ⁰	15 ¹	15 ²	16 ⁰	16 ¹	16 ²	17 ⁰	17 ¹	17 ²	
1916	7	—	2	1	2	11	10	12	29	50	67	72	58	87	16	8	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
53	—	—	4	6	9	20	32	42	49	46	26	27	16	5	5	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
48	—	—	1	4	14	15	25	42	56	53	55	31	13	5	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
41	1	2	2	3	7	13	22	25	36	43	40	45	26	5	8	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
34	—	—	—	—	—	—	—	2	3	—	7	16	6	8	21	25	9	20	7	11	4	4	4	—	—	—	—	—	—	—	—	—
12	—	—	—	3	2	4	12	19	23	39	41	42	40	37	26	24	19	12	10	5	6	3	—	—	—	—	—	—	—	—	—	—
17	—	—	—	—	3	1	7	12	29	41	52	56	52	48	34	36	25	22	13	10	7	2	3	1	1	—	—	—	—	—	—	—
22	—	—	—	—	—	—	2	2	1	2	4	11	11	15	35	33	31	39	31	39	20	16	4	2	1	1	—	—	—	—	—	—
1917	63	—	—	—	—	2	4	5	10	13	35	55	74	63	51	36	24	5	1	—	—	—	—	—	—	—	—	—	—	—	—	—
64	—	—	—	—	—	—	1	6	7	23	40	54	65	63	42	43	15	10	6	—	—	—	—	—	—	—	—	—	—	—	—	—
65	—	—	—	—	—	1	—	4	12	22	51	67	56	55	52	33	20	8	6	—	1	—	—	—	—	—	—	—	—	—	—	—
66	—	—	—	—	—	—	1	1	12	21	44	61	51	63	50	25	23	19	9	2	1	—	—	—	—	—	—	—	—	—	—	—
1918	49	—	5	2	9	13	29	28	32	32	31	28	34	18	15	9	7	9	3	—	—	—	—	—	—	—	—	—	—	—	—	—
50	—	—	1	3	4	6	22	19	26	25	33	38	26	32	18	11	8	6	2	—	—	—	—	—	—	—	—	—	—	—	—	—
51	—	—	1	1	3	4	10	20	29	43	60	60	48	46	28	20	8	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—
52	—	—	1	4	6	9	14	20	27	29	35	57	45	48	22	27	8	2	1	2	—	—	—	—	—	—	—	—	—	—	—	—
53	—	1	3	4	13	13	19	27	27	53	51	48	29	25	22	9	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—
54	—	2	—	2	6	9	13	16	33	30	37	44	30	40	15	18	10	4	3	—	1	—	—	—	—	—	—	—	—	—	—	—
3	1	6	4	3	15	14	32	38	28	35	46	41	40	26	16	10	3	4	1	1	—	—	—	—	—	—	—	—	—	—	—	—
4	—	1	5	4	10	10	19	14	19	32	27	37	39	33	15	16	13	6	7	1	—	—	—	—	—	—	—	—	—	—	—	—
46	—	—	—	—	—	—	—	—	1	4	6	8	10	18	18	14	21	15	10	8	1	—	—	—	—	—	—	—	—	—	—	—
47	—	—	—	—	—	—	—	1	—	1	3	5	9	6	6	12	10	8	10	7	7	3	—	—	—	—	—	—	—	—	—	—
48	—	—	—	—	—	—	—	4	6	14	8	10	22	15	15	26	30	20	13	16	5	1	1	—	—	—	—	—	—	—	—	—
55	—	—	—	—	—	—	—	1	4	5	5	14	12	18	28	27	31	23	16	12	8	3	—	1	1	—	—	—	—	—	—	—
56	—	—	—	—	—	—	1	3	2	2	15	10	22	23	26	18	23	19	16	23	3	9	7	3	1	—	—	—	—	—	—	—

Curves of Lengths of Group 5.

Year	row	No. of																																		
		9 ²	9 ³	10 ⁰	10 ¹	10 ²	10 ³	11 ⁰	11 ¹	11 ²	11 ³	12 ⁰	12 ¹	12 ²	13 ⁰	13 ¹	13 ²	13 ³	14 ⁰	14 ¹	14 ²	14 ³	15 ⁰	15 ¹	15 ²	15 ³	16 ⁰	16 ¹	16 ²	16 ³	17 ⁰	17 ¹	17 ²			
1916	3	—	—	2	1	8	12	15	19	34	39	37	50	42	28	17	9	2	3	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	
	8	—	—	—	—	—	1	6	5	10	29	34	64	49	35	35	20	19	9	3	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	
	13	—	—	1	2	1	12	18	30	33	40	50	40	22	27	18	20	9	5	17	3	2	1	1	—	—	—	—	—	—	—	—	—	—	—	
	18	—	—	—	1	4	7	7	11	11	28	43	47	47	57	40	40	37	13	16	8	7	2	2	—	—	—	—	—	—	—	—	—	—	—	
	23	—	—	—	—	—	—	—	—	1	8	9	20	33	29	37	33	24	28	31	24	6	6	5	1	—	—	—	—	—	—	—	—	—	—	
	30	—	—	1	1	1	2	3	12	16	47	54	51	47	55	52	23	22	14	14	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	35	—	—	—	—	—	3	9	6	7	19	18	31	35	33	16	28	20	16	15	2	2	3	—	—	—	—	—	—	—	—	—	—	—	—	
	40	—	—	—	—	—	—	—	—	—	4	5	11	10	21	14	23	25	21	14	9	7	1	—	—	—	—	—	—	—	—	—	—	—	—	
	45	—	1	3	7	15	27	36	33	30	26	32	15	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	50	—	—	1	1	1	6	9	13	28	32	24	31	18	12	18	10	13	5	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
1917	15	—	—	—	—	—	—	—	—	12	25	41	51	59	56	28	13	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	16	—	—	—	—	—	—	—	—	6	7	14	19	21	30	23	22	22	31	11	17	18	8	8	2	1	—	—	—	—	—	—	—	—	—	
	19	—	—	—	—	—	2	—	1	9	19	31	53	57	64	57	32	19	9	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	20	—	—	—	—	—	—	2	5	6	11	38	37	48	35	39	22	18	16	11	6	2	1	1	—	—	—	—	—	—	—	—	—	—	—	
	21	—	—	—	—	—	—	1	4	11	13	22	29	37	46	42	27	22	12	8	4	4	8	7	1	4	—	1	—	—	—	—	—	—		
	22	—	—	—	—	—	—	—	—	1	3	2	2	11	9	17	23	28	27	27	29	13	23	15	13	9	1	3	1	—	—	—	—	—		
	23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
	24	—	—	—	—	—	—	—	—	4	3	10	14	42	33	35	28	21	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	25	—	—	—	—	—	—	—	—	—	2	11	12	15	18	35	29	31	5	15	14	17	11	8	4	—	1	1	1	—	—	—	—	—	—	
	26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
27	—	—	—	—	—	—	—	—	5	9	12	28	36	49	44	61	39	21	14	1	3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	
28	—	—	—	—	—	—	—	—	1	4	9	18	29	35	43	61	51	13	21	22	7	1	6	—	—	—	—	—	—	—	—	—	—	—	—	
29	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
30	—	—	—	—	—	—	—	—	—	2	7	19	32	52	60	44	49	32	12	5	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	
1918	31	—	—	—	—	—	—	—	—	1	1	6	13	21	30	21	32	34	12	4	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	32	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	34	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	38	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	39	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	40	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	41	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	44	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
	45	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	

Curves of Lengths of Group 9.

Series of Lengths of Group 3.																																		
No. of Year row	4 ^e	3 ^e	10 ⁰	10 ¹	10 ²	10 ³	11 ⁰	11 ¹	11 ²	11 ³	12 ⁰	12 ¹	12 ²	12 ³	13 ⁰	13 ¹	13 ²	13 ³	14 ⁰	14 ¹	14 ²	14 ³	15 ⁰	15 ¹	15 ²	15 ³	16 ⁰	16 ¹	16 ²	16 ³	17 ⁰	17 ¹	17 ²	
1916	4	—	—	—	—	—	6	7	17	14	12	22	38	41	30	40	23	23	12	4	1	—	2	—	—	—	—	—	—	—	—	—	—	—
	9	—	1	—	—	—	4	4	13	11	20	18	42	36	47	39	43	40	22	10	6	3	1	—	—	—	—	—	—	—	—	—	—	—
	19	—	—	—	—	—	3	3	10	17	21	39	34	43	38	50	51	37	29	18	4	5	2	—	—	—	—	—	—	—	—	—	—	—
	27	—	—	—	—	—	—	—	8	6	12	20	23	35	50	36	40	39	43	29	20	10	8	1	1	—	—	—	—	—	—	—	—	—
	31	—	—	—	—	—	1	1	5	22	18	20	26	29	36	46	32	21	6	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	36	—	—	—	—	—	6	7	15	21	19	23	32	23	28	37	30	22	9	8	2	1	—	—	—	—	—	—	—	—	—	—	—	—
	51	—	—	—	—	—	—	4	4	3	6	14	16	26	30	17	17	8	4	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—
1917	43	—	—	—	—	—	—	—	1	4	4	3	6	7	24	33	26	30	28	45	38	27	22	19	14	3	2	3	4	—	—	—	—	—
	44	—	—	—	—	—	—	—	1	1	1	5	11	16	13	21	12	14	16	9	8	6	5	4	—	—	—	—	—	—	—	—	—	—
	45	—	—	—	—	—	1	—	1	2	2	10	6	16	21	25	18	30	16	12	7	1	2	2	2	1	—	—	—	—	—	—	—	—
	46	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	47	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	48	—	—	—	—	—	—	—	1	2	11	14	15	30	29	41	36	42	20	28	15	5	2	4	2	—	—	—	—	—	—	—	—	—
	49	—	—	—	—	—	—	—	1	—	5	7	10	17	10	20	21	27	26	43	42	19	20	15	16	5	2	3	—	—	—	—	—	—
	52	—	—	—	—	—	—	—	1	1	1	11	14	19	29	33	33	34	43	18	17	6	6	4	2	1	2	—	—	—	—	—	—	—
	53	—	—	—	—	—	—	—	1	—	1	4	13	20	26	24	47	31	49	35	40	19	16	12	8	3	—	—	—	—	—	—	—	—
	54	—	—	—	—	—	—	—	1	1	1	4	6	12	26	19	27	21	29	31	16	21	17	11	5	3	4	1	—	—	—	—	—	—
	55	—	—	—	—	—	—	—	—	—	1	1	8	10	22	28	28	29	25	21	20	16	4	7	3	2	—	—	—	—	—	—	—	—
	56	—	—	—	—	—	—	—	—	—	1	1	4	11	16	17	37	21	33	22	30	16	11	6	3	3	—	—	—	—	—	—	—	—
	57	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	58	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	59	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	60	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	61	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	62	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1918	19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	20	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	61	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	62	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	58	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Numbers indicate rows in the various years; *letters*, plants. In connection with plants the *italic letters* show that they were selected as *X*, *E*, *M*, etc.; in connection with rows they indicate the behaviour of the row as a whole.

The *italic figures* denote the numbers of non-*M* and *M* plants.

Genealogical Table of $E \times M$.

	43			44	45					46			47	48		
1914	c	g	j	l	f	h	i	k	m	b	c	i	c	b	f	h
	<i>M</i>	<i>E</i>	<i>X</i>	<i>M</i>	<i>M</i>	<i>X</i>	<i>E</i>	<i>M</i>	<i>E</i>	<i>E</i>	<i>E</i>	<i>int.</i>	<i>E</i>	<i>E</i>	<i>M</i>	<i>M</i>
	3	7	4	15	19	6	8	{10 16}	12	5	14	9	17	21	18	{20 22}
1915	<i>M</i>	13/9	<i>X</i>	<i>M</i>	<i>M</i>	<i>X</i>	17/5	<i>M</i>	17/7	18/2	15/7	<i>int.</i>	16/5	16/3	<i>M</i>	<i>M</i>
																{20 22}
								Groups :	12	5	14	9		21	18	{20 22}

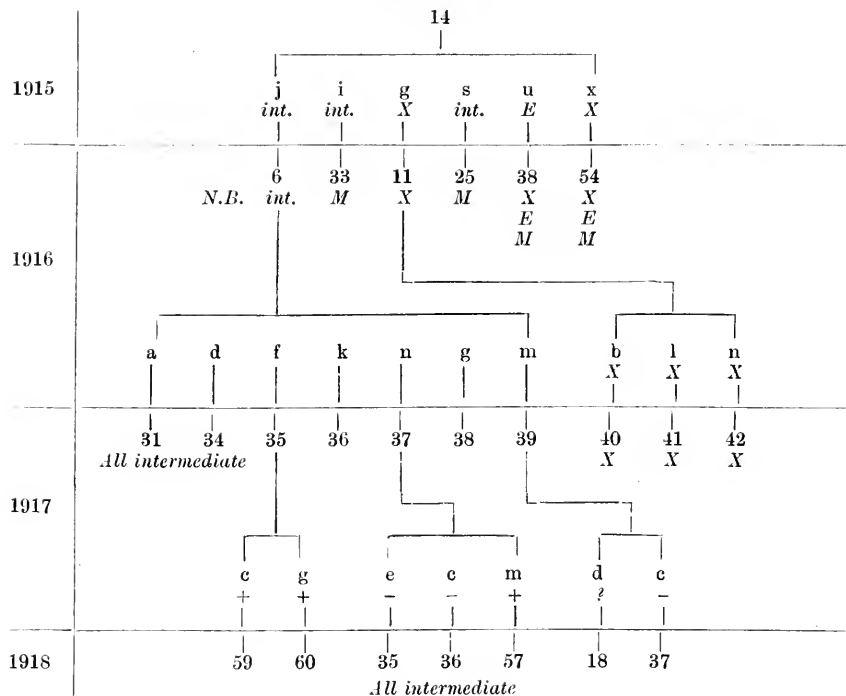
$$\text{Total of } \frac{\text{non-}Ms}{Ms} = \frac{112}{38}$$

Group 21.

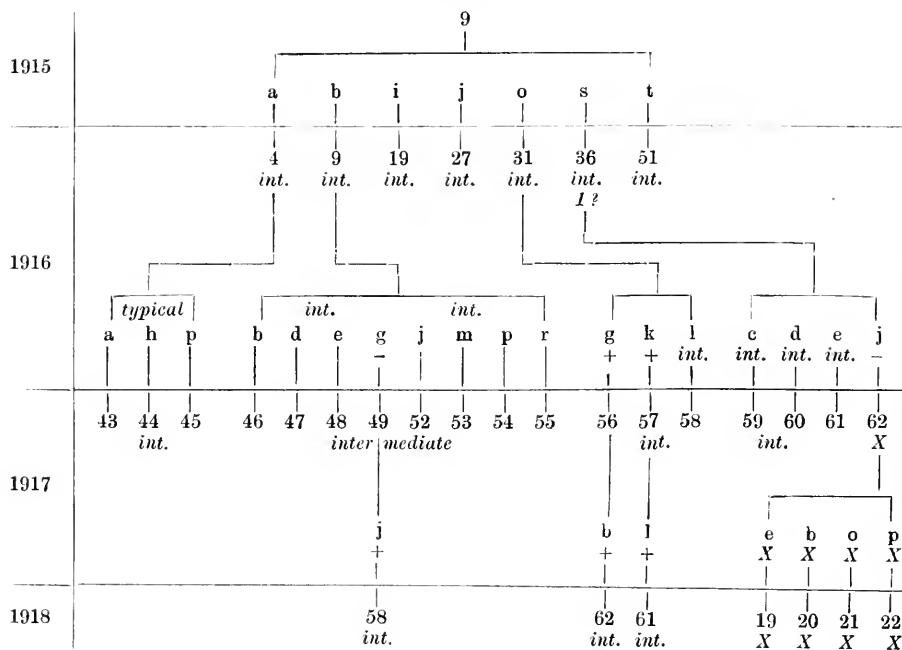
	<div style="text-align: center;">21</div> <div style="display: flex; justify-content: space-around;"> <div>l X 7 X</div> <div>a X 53 X</div> <div>g X 48 X</div> <div>h X 41 X</div> <div>i M 34 M</div> <div>m E 12 X E M</div> <div>o E 17 X E M</div> <div>s M 22 M</div> </div>									
1915										
1916	<div style="display: flex; justify-content: space-around;"> <div>f + 63</div> <div>g - 64</div> <div>h - 65</div> <div>p - 66</div> </div>									
1917	<div style="display: flex; justify-content: space-around;"> <div> <div>b - 3</div> <div>h + 4</div> </div> <div> <div>a - 49</div> <div>m + 50</div> </div> <div> <div>j - 51</div> <div>e + 52</div> </div> <div> <div>m - 53</div> <div>b + 54</div> </div> <div> <div>e 46</div> <div>l 47</div> <div>g 48</div> <div>f 55</div> <div>c 56</div> </div> </div>									
1918	<div style="display: flex; justify-content: space-around;"> <div>No difference</div> <div>All M</div> </div>									

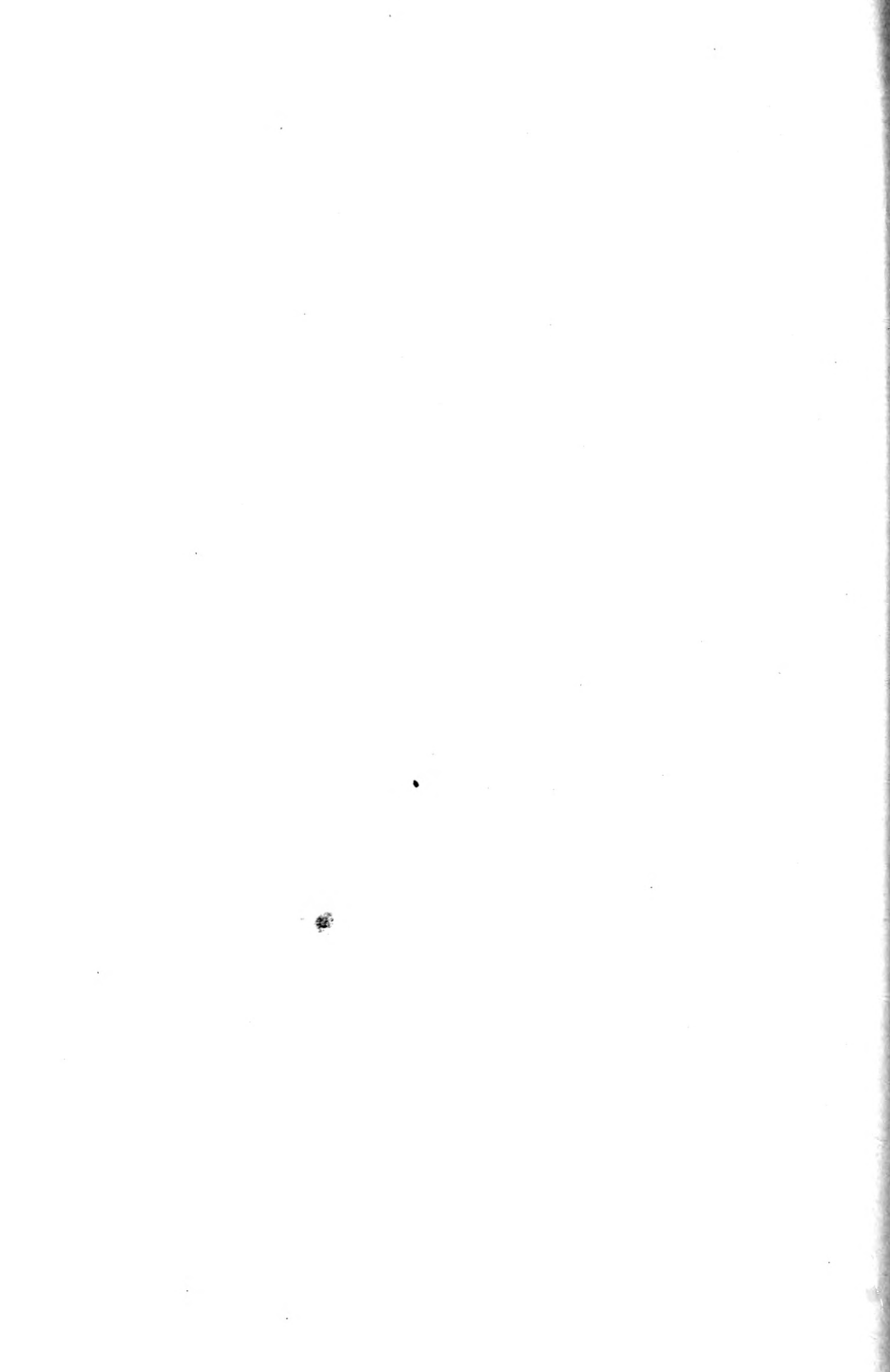
204 Segregation of a Quantitative Character in Beans

Group 14.



Group 9.





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The *Journal of Genetics* is a periodical for the publication of records of original research in Heredity, Variation and allied subjects. The Journal will also, from time to time, contain articles summarising the existing state of knowledge in the various branches of Genetics, but reviews and abstracts of work published elsewhere will not, as a rule, be included. It will be issued in parts as material accumulates, and a volume will consist of three such parts.

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ARTHUR BALFOUR PROFESSOR OF GENETICS IN THE UNIVERSITY OF CAMBRIDGE



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DWARF FORMS IN BARLEY.

BY BUNGO MIYAZAWA.

(With Plate XX.)

WITH the object of barley breeding a number of F_1 plants between *Goldenmelon*¹ and the Japanese variety called *Sekitori* were grown in 1914 at the Agricultural Experiment Station, Kanagawa-Ken, Japan. One of these F_1 plants was crossed back by *Goldenmelon* in that year, and a dwarf plant appeared in 1915 among the 96 offspring resulting from this back-cross. As the hereditary behaviour of this dwarf may be of some interest I am going to describe here briefly the results of my investigations. The characters of this plant, together with those of its parents, are as follows:

	<i>Goldenmelon</i>	<i>Sekitori</i>	Dwarf plant
Height of plant ...	tall	short	less than <i>Sekitori</i>
Rows in ear ...	two	six	two
Length of awns ...	long	short	long
Time of ripening ...	late	early	later than in <i>Goldenmelon</i>

Although this dwarf plant produced shoots more abundantly than we have ever seen in any variety, over half of the shoots thus developed failed to produce ears; and moreover they were smaller than either of the two parents in various respects, as length and width of leaf, size of kernels, etc.

In November 1915 about 40 seeds of this dwarf plant were sown, almost all of which came to germination, but towards January or February 1916 some died, and only 24 completed their growth. Of the latter three types are easily distinguished with respect to the height of plant, length of ear and awn, etc., each of which contains in its turn normal and dwarf forms, so that we have altogether three kinds of normals and three kinds of dwarfs. Below I will classify all these simply into two classes, viz. normal and dwarf. According to this classification the 24 plants above cited consist of 18 dwarf and 6 normal individuals, whence

¹ Though this variety is here called by this name, it seems that it differs from real *Goldenmelon*.

we might perhaps be led to the false conclusion that we were dealing here with the 3:1 segregation. In November 1916 seeds taken from 9 dwarf and 6 normal plants were sown; in 1917 all dwarfs were observed to undergo segregation, the offspring from 9 dwarf plants containing altogether 292 dwarfs and 161 normals, i.e. 64.5 and 35.5 per cent. respectively, whilst all normal plants were found to breed true to their type.

From the experiments above stated we see firstly that the normal type is recessive to the dwarf, and secondly that all dwarf plants are of heterozygous constitution. Were the segregation observed in 1916 of the 3:1 type, only six out of nine families of dwarfs should be heterozygous. Moreover, as the ratio of dwarfs and normals in 1917 is approximately equal to 2:1 (= 292:161), it is clear that we are not dealing here with a typical 3:1 segregation.

The experiments of the two following years, viz. 1918 and 1919, fully confirm what was said above. Thus all the offspring of dwarf plants underwent segregation into dwarfs and normals in the ratio indicated in the following table:

			Dwarfs	Normals	Totals
Results in 1918	...		599	304	903
„ 1919	...		748	375	1123
Totals	1347	679	2026
Expected	...		1350.66	675.33	—

From the above results we see that the ratio of dwarfs and normals is approximately 2:1. On the contrary all offspring derived from normal plants produced only normal plants.

Furthermore, various crosses were made between the offspring, and also between them and either one of the two original parents, or other normal varieties. The details of these crosses will be omitted here; it will suffice to say that the results corresponded exactly to expectation.

Ph. De Vilmorin¹ has studied the inheritance of dwarf forms in wheat. He obtained two dwarfs against one normal and came to the probable conclusion that such a result might be caused by the fact that any zygote homozygous in respect to dwarfness is either not produced, or, if produced, dies very early.

Now I have entertained the view that our case, which is very similar to that described by Vilmorin, might be explained by either one of two alternatives below stated, viz. (1) seeds containing zygotes homozygous in respect to dwarfness do not germinate at all, or (2) they die off soon

¹ "Sur une Race de blé nain inflexible." *Journal of Genetics*, Vol. III. 1913, pp. 67—76.

after their germination. To decide between these two alternatives, experiments were devised to test the germinating power of the seeds: they were sown in a Petri dish containing sand, as well as in the field; the result was that almost all seeds were perfectly viable, because the rate of their germination was 90 per cent. or even more. The first alternative was thus proved to be untenable. Now to pass to the second: since some young seedlings might die from the severe cold of January and February, some seeds derived from dwarf and normal plants were sown in pots late January 1919 and placed in a cold frame to protect them against severe cold. A certain number of seedlings were transplanted into the field March 1st, because the frost in this month is generally only slight in the vicinity of our Experiment Station, and various plants, especially barley, begin then to grow vigorously, so that there is no more danger of their suffering from severe cold. In late April I discovered among these plants a quite new dwarf form, very different from the dwarf described above. This new form produces a great many young shoots; thus in some cases 152 shoots were counted in a stock; its growth is very slow, so that even in late April, when the ordinary dwarf plants have attained their proper height and are already ready to produce their ear, we could hardly see in the new form any indication of the production of the ears. Its height too was so low as to be easily mistaken for some other graminaceous plant (see Pl. XX. fig. 1). Even in late May or early June none of these plants had produced any ear. All were seriously attacked by *Erysiphe graminis* and their growth became gradually poorer. By the middle of June almost all of them died, whereas the other two types had completed their growth. This new dwarf type which is unable to produce an ear I shall call *sterile-dwarf* in contradistinction to ordinary dwarf forms.

The segregation observed in 1919 was as follows:

		Sterile-dwarf	Dwarf	Normal	Total
Actual	...	71	172	80	323
Expected	...	80.75	161.50	80.75	—

We may therefore conclude as follows: even in the experiments of 1916, 1917, 1918, and 1919 a certain number of sterile-dwarf plants must have appeared, but all of them died early under severe cold on account of their weak constitution, so that they escaped our observation. In the experiment in which the seeds were sown in January 1919 they were however protected against it and saved, so that they came under our observation.

The above conclusion was perfectly confirmed by the following breeding experiment: a certain number of seeds of ordinary dwarf plants were sown in early spring 1919 instead of the autumn of the preceding year as it is usually the case in Japan. By this method I was enabled to observe the segregation into three forms just discussed very easily, and the numerical results were as follows:

		Sterile-dwarf	Dwarf	Normal	Total
Actual	156	340	188	684
Expected	...	171	342	171	—

The ratio of the three types is approximately 1:2:1. The number of sterile-dwarf plants, however, is in both cases somewhat smaller than might be expected theoretically; this may be ascribed to the fact that they die more easily than the others on account of their weak constitution.

Thus we reach the conclusion that the dwarf plant which was found at the beginning of my experiments was heterozygous with respect to the characters in question, and that it was intermediate externally, i.e. smaller than normal, but taller than sterile-dwarf. In other words, if we denote the allelomorph for dwarfness by **D** and its absence by **d**, we have sterile-dwarf = **DD**, normal = **dd**, and ordinary dwarf = **Dd**. The seed which first gave rise to the dwarf plant **Dd** may perhaps have arisen from **dd** by mutation. Cases similar to ours have been observed in respect of dwarf forms in plants. This is however the first case recorded in which the sterile-dwarf has appeared in addition to the ordinary dwarf.

EXPLANATION OF PLATE XX.

Fig. 1. On the left two sterile-dwarf plants; one plant in the middle is normal and two plants at right are ordinary dwarf types.

Fig. 2. In the middle is a normal plant and on either side are dwarf plants of the same type. The characters of these plants are very different from those shown in Fig. 1, and this is one of the three types mentioned on page 205.

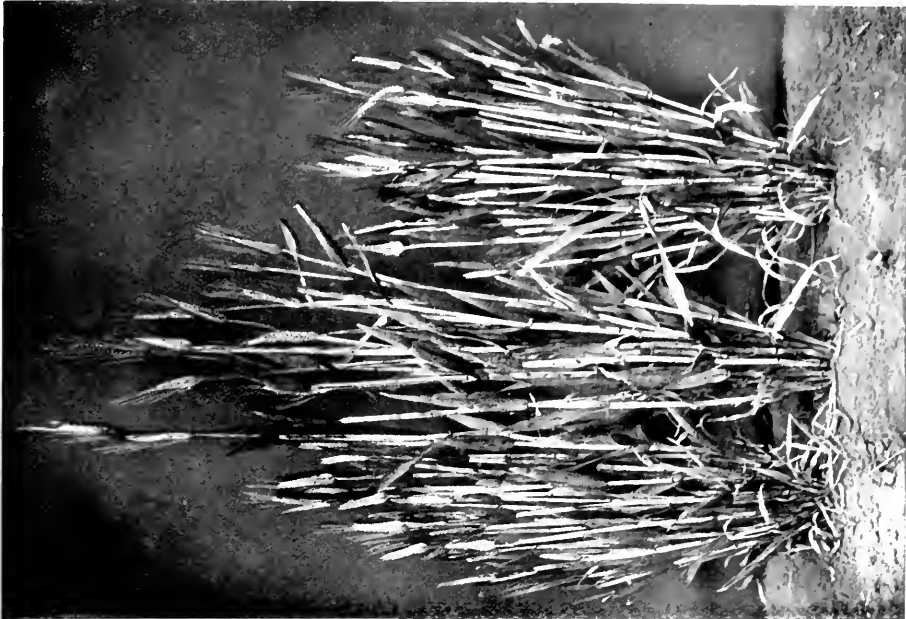


Fig. 2.



Fig. 1.



NOTE ON THE DETECTION OF SEGREGATION BY EXAMINATION OF THE POLLEN OF RICE.

By F. R. PARNELL.

(With Plate XXI.)

Glutinous Rice.

FOR several years a study has been in progress on the inheritance of the (so-called) *glutinous* character typical of a small group of cultivated varieties of rice. These varieties differ from the ordinary *starchy* type in that the grain becomes gelatinous when cooked in water, so much so that if boiled in the ordinary way the result is a sticky mass resembling glue.

Glutinous grains can be distinguished by their appearance since the endosperm is dead white, giving a fracture like porcelain, whereas in starchy grains it is always more or less translucent.

Microscopic examination of sections of the endosperm shows no marked difference between the two types, the cells in both cases being filled with the highly compound starch grains characteristic of rice. The action of iodine, however, brings out a very sharp distinction—the starch grains of ordinary starchy varieties take on the usual deep blue colour, whereas those of glutinous varieties become reddish in dilute iodine, passing through wine colour to dark brown as the strength of the solution is increased. The same difference is seen when grains are broken across and dipped into iodine solution.

The production of a reddish colour with iodine is characteristic of amyloextrine, a rare form of starch that occurs in mace, and it is presumably the presence of this form of starch that gives to glutinous rices their special character.

Inheritance.

In inheritance the glutinous character behaves as a simple recessive to starchy but, since double fertilization takes place, the endosperm is a fertilization product and the usual complication of results is obtained.

Thus when flowers of a glutinous plant are fertilized with starchy pollen they produce grains with starchy endosperm. An F_1 plant, selfed,

bears a mixture of starchy and glutinous grains. These give rise in F_2 to three groups of plants, bearing respectively—all starchy grains, all glutinous, and a mixture of starchy and glutinous as in F_1 . Those bearing all starchy or all glutinous grains breed true to these characters in F_3 , whereas those which bear the mixture give the three groups again in F_3 .

The mixture of grains on an F_1 plant should give a simple 3 : 1 ratio of *starchy* to *glutinous*. This ratio is approached fairly nearly in the numbers recorded, though there is always a slight excess of starchy. For nine plants, each giving about the same ratio, the following total figures were obtained :

		Starchy grains	Glutinous grains
Total of 9 plants	.	5,292	1,587
Expectation 3 : 1	...	5,159	: 1,720

In F_2 the three groups of plants would be expected to give a 1 : 2 : 1 ratio of *starchy* : *mixture* : *glutinous*. In the families so far raised there is a very considerable departure from this ratio as shown by the following figures :

		All starchy	Mixture	All glutinous
Total of 81 families	...	9,211	13,729	5,021
Expectation 1 : 2 : 1	...	6,990	: 13,980	: 6,990

It appears most probable that the single factor explanation of the difference between starchy and glutinous is correct but that some disturbing influence affects the ratios in F_2 . There are a number of possibilities in this direction and some of these are being investigated. Certain preliminary results suggest that differential germination and dying-off may be responsible.

Pollen Dimorphism.

In searching for some explanation of the F_2 ratios an examination was made of the pollen on F_1 plants. With a view to distinguishing the two genetic types the pollen was treated with iodine. The result was most satisfactory—two distinct types became evident, one giving the dark blue reaction of ordinary starch and the other the reddish reaction of amylopectine. With iodine solution of the right strength a very sharp distinction can be obtained since the starchy grains become dark blue whilst the others remain only yellowish.

Pollen from the two pure parents was then examined in iodine solution. The starchy parent gave only the blue type of pollen; the glutinous parent gave the reddish type.

Plate XXI shows photographs of whole anthers of the two parents and F_1 . These were mounted in chloral hydrate solution containing iodine, which shows up the pollen grains very well. Part of an F_1 anther is also shown more highly magnified, as also some free F_1 pollen mounted in plain iodine solution.

There can be no doubt that the two types recognizable in F_1 pollen represent the two genetic types produced by segregation. It thus becomes possible to keep some track of segregation and to determine the relative proportions of the two types of gamete in different plants, flowers, anthers, etc.

Examination shows that the two types occur mixed throughout all parts of each pollen sac. Counts were made of the number of pollen grains of each type in various anthers, the latter being teased out in a drop of iodine solution in such a manner that every developed grain could be distinguished. There was some variation in the proportions of the two types and the ratio was rather more uniform for anthers in the same flower than for anthers from different flowers of the same plant. In eighteen anthers, from three plants, the starchy pollen varied from 43.2% to 51.8%, the average being 48.1%.

An attempt was made to determine at what stage in spermatogenesis segregation occurred. When this work was started the main flowering was finished and only very poor material was available. It appears, however, that there is little hope of success in this direction owing to the absence of starch in the early stages. Pollen mother cells in various stages of division were examined but no trace of starch could be detected. The pollen grains themselves show no starch until they are well developed and beginning to lay down reserve materials.

A further examination will be made of better material from a crop that is now being grown. It is hoped also, if time permits, to look for a similar indication of segregation in oogenesis.

A paper has recently been seen in which Bateson¹ refers to the work of Renner² who detected dimorphism, due to genetic segregation, in the pollen of *Oenothera*. The author has seen only a short abstract of this work stating that the differences noted were in respect to size of pollen grains and shape of their included starch grains.

It is probable that a systematic search in other plants would reveal many cases of similar dimorphism in pollen, e.g. in the form of starch,

¹ Bateson, W., "Genetic Segregation." *American Naturalist*, Vol. LV. No. 636, January—February, 1921.

² Renner, O., *Ber. Deutsch. Bot. Gesell.* Bd. XXXVII. (1919), No. 2, p. 129.

its presence and absence, or the presence and absence of other substances recognizable by microchemical tests. This line of work appears to offer distinct possibilities from the point of view of determining the stage at which segregation takes place, especially if such dimorphism can be found in a species in which the pollen grains remain united in tetrads.

DESCRIPTION OF PLATE XXI.

Iodine Reaction of Starch in Pollen Grains.

- Fig. 1. Anther of *starchy* type, pollen all dark.
- Fig. 2. Anther of *glutinous* type, pollen all light.
- Fig. 3. Anther of F_1 , pollen mixture of dark and light.
- Fig. 4. Part of F_1 anther more highly magnified.
- Fig. 5. Free pollen of F_1 showing two types.



Fig. 1.

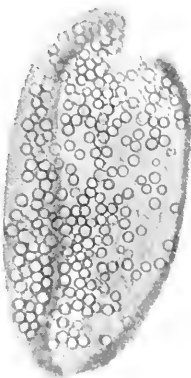


Fig. 2.



Fig. 3.

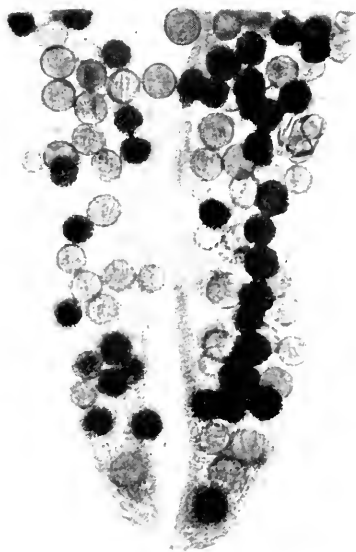


Fig. 4.

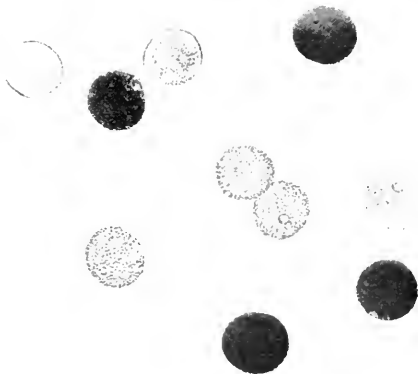


Fig. 5.



NOTES ON THE CYTOLOGY AND GENETICS OF THE GENUS FUCHSIA.

By RUDOLPH BEER, B.Sc., F.L.S.

(With Plates XXII—XXIV.)

IN contrast to the extensive literature which has grown up round the cytology and genetics of *Oenothera* very little work has been done upon these subjects in the case of the Fuchsias. In 1850 Wimmel (17) called attention to the irregularities in the number and size of the pollen grains produced from the mother-cell of Fuchsia and in 1886 Wille (16) made further observations upon the same subject. He counted five to fourteen microspores arising from a single mother-cell. He explained the occurrence of these supernumerary pollen grains by assuming that "In dem Falle, wo bei Fuchsia sp. sieben Zellen entstanden waren, konnte ich nicht dartüber im Zweifel sein, das diese daher kam, dass drei der Zellkerne der Tetrade noch sich einmal getheilt hatten, ehe die Cellulosequerwände ausgebildet waren, während der Vierte ungetheilt blieb" (16 p. 61). Where five or six microspores were produced he believed the explanation to be similar. In the case of the higher numbers (e.g. 14) he was unable to follow the cell-divisions, and was uncertain whether the additional pollen grains are due to secondary divisions of one pollen mother-cell alone or whether they are to be derived from two or more primitive mother-cells which have not become separated from one another in the usual manner.

In 1907 the present writer (1) published a short note upon "The Supernumerary Pollen Grains of Fuchsia and their mode of development." It was found that the abnormal numbers of pollen grains which develop from the mother-cells is due to the irregular distribution of the chromosomes during the first meiotic division and that no evidence could be found to support Wille's explanation of the phenomenon.

In 1912 Bonnet (3) published an account of the tapetal cells of certain Angiosperms and included those of Fuchsia among the number.

Beyond this I can find no literature dealing with the cytology of Fuchsias.

Some time ago I continued my studies of the cytological features which are connected with the development of supernumerary pollen grains in certain species and hybrids of *Fuchsia* and concurrently I began a series of observations upon the genetics of the genus. Circumstances have intervened and prevented the completion of the work, but it was thought that it might be useful to future workers if a brief statement were made of such results as were obtained, and of the lines of work which appeared to promise interesting results.

A. *Cytology of Fuchsias.*

I will first describe the facts which are to be seen in a hybrid form known as "Alice Hoffman."

The early stages of the first meiotic division in the pollen sacs take place in a normal manner as will be seen from Pl. XXII, figs. 1—8. The spindle which develops is apolar and the chromosomes become arranged regularly at its equator at the conclusion of the prophase.

During the anaphase, however, the chromosomes move very irregularly towards the spindle poles and some, either singly or in groups, lag behind the rest, and often become entirely cut off from the two main chromosome groups. This irregular distribution of the chromosomes is shown in figs. 9 and 10. At the conclusion of the division these scattered and separated chromosomes behave variously. In the majority of cases distinct nuclei are developed in association with them. In some instances only a single chromosome may become organised into a small nucleus, but more commonly small groups of two or more chromosomes are associated together in the development of a nucleus. The size of the nucleus which is formed depends upon the number of chromosomes which enter into it. Examples of such nuclei can be seen in figs. 11 and 12. In several cases the chromosomes were so scattered at the beginning of the telophase that they did not lead to the formation of a number of separate nuclei, but they all became included within a single, large, irregular nucleus. In fig. 12 one small nucleus is seen to have developed round a chromosome which had become widely separated from its fellows, whilst all the remaining chromosomes were included in the large irregular nuclear body which occupies the centre of the mother-cell. Whilst it is more usual to find nuclei organised round the scattered chromosomes there are other instances in which these bodies degenerate without giving rise to a nucleus. In fig. 13 the chromosomes excluded from the two principal groups are probably about to undergo degeneration. All the nuclei, both small and large alike, enter upon the

second meiotic division in the usual manner. Spindles, varying in size with the number of chromosomes, are developed in association with each nucleus, and the course of mitosis proceeds in quite a normal manner. No irregularities in the distribution of the daughter-chromosomes are to be seen in this division.

Pl. XXII, fig. 17 gives a representation of the second meiotic division. Single chromosomes each associated with a small spindle can be seen in fig. 14. In Pl. XXIII, fig. 16 we have a case which probably represents the second division of one of the large, irregular nuclei referred to above and represented in fig. 12.

The nuclear divisions which have been described in the foregoing account are followed by the division of the cells so that each nucleus becomes associated with a distinct cell.

Pl. XXIII, fig. 19 represents a mother-cell which has divided up in this manner to form the initials of a number of pollen grains.

In fig. 18 ten pollen grains will be seen to have developed from a single mother-cell.

It is readily apparent that the size of the pollen cell is dependent upon the size of the nucleus with which it is associated and this, in turn, depends upon the number of chromosomes which enter into its composition. The details of this relationship will not, however, be dealt with in the present paper.

From what has been said above it will be seen that no evidence was found of the existence of secondary divisions of the cells such as Wille described, nor do the present observations give any support to this author's suggestion that a fusion (or non-separation) of primitive mother-cells might occur in those cases in which the supernumerary microspores were very numerous.

In addition to the variety "Alice Hoffman" the meiotic divisions of *Fuchsia globosa* and *Fuchsia corallina* were studied in detail. In both these plants more than the normal number of four microspores are produced from each pollen mother-cell. It was found that the distribution of the chromosomes during the first meiotic division is quite similar to that taking place in "Alice Hoffman" and that single chromosomes, or small groups of them, become separated from the rest, and usually give rise to small nuclei. Here also some of the isolated chromosomes may fail to organise nuclei, but undergo degeneration instead. It will be unnecessary to describe the details of meiosis in these two forms, but it will be sufficient to call attention to Pl. XXIII, figs. 20—24 which represent the principal facts of interest.

The pollen grains of *Fuchsias* follow the general Onagraceous type. Their membrane consists of an exospore, a mesospore, and an endospore, and is furnished with two or more interstitial bodies. The *Fuchsias* have been divided into two groups according to whether their pollen grains possess two or three interstitial bodies. *Fuchsia globosa* is a typical example of the group which possesses three interstitial bodies upon each pollen grain, whilst *Fuchsia procumbens* has pollen grains with only two interstitial bodies.

Whilst these numbers are characteristic of the majority of fertile pollen grains in each case, yet they are not constant in those instances in which irregular pollen development takes place. In these cases the number of interstitial bodies appears to vary with the size of the pollen grain, and in some of the smaller grains only a single interstitial body is formed. Fig. 27 shows such a small, supernumerary pollen grain with only a single interstitial body. Although not shown in this figure, these small pollen grains, apart from the number of interstitial bodies they possess, have membranes which are identical in structure and chemical composition with those of the larger grains.

We have already seen that the distribution of the chromosomes to the pollen grains is an irregular one, and that the small grains receive only a small proportion of their normal number of chromosomes.

Notwithstanding this all the pollen grains develop walls which are characteristic of the genus both in structure and chemical composition. These facts have an interesting bearing upon the theory of the localisation of generic and specific characters in particular chromosomes, since the chromosomes which any particular pollen grain receives is perfectly haphazard in the present instance. The explanation is probably similar to the one which has been suggested in the case of the development of certain animal eggs in which the cytoplasm becomes set to a definite line of development at an early stage. We may probably assume that the cytoplasm of the pollen mother-cell has already been set, through the influence of the still undivided nucleus, to a definite course of development, and that it already has the mechanism implanted in it for the formation of pollen membranes of a definite structural and chemical constitution. It is a matter of secondary importance for carrying out the work which is allotted to it at an early stage how the chromosomes subsequently become distributed at the meiotic division, or how it becomes divided up at the conclusion of that division.

From the foregoing account it will be seen that the development of abnormal numbers of pollen grains from the mother-cells depends upon

the existence of irregularities in the distribution of the chromosomes during the meiotic divisions.

Observations have been made to determine the extent of the occurrence of such irregularities of pollen development in a number of species and hybrids of *Fuchsia* with the following results:

A. *Forms with irregular pollen development or all sterile pollen.*

Fuchsia globosa.

F. corallina.

F. exorticata.

F. parviflora (no pollen development; anthers collapsed).

F. Cottinghami (no pollen development; anthers collapsed).

F. macrostemma, var. *conica*.

F. macrostemma, var. *discolor*.

F. simplicicaulis (most marked early in the season).

F. arborescens.

F. Riccartoni.

F. virgata × *F. fulgens* (3 *N*).

F. virgata × *F. fulgens* (3 *P*).

B. *Forms with regular pollen development*

Fuchsia fulgens.

F. procumbens.

F. gracilis.

F. reflexa.

F. virgata.

F. myrtifolia.

F. alpestris.

F. pumila.

F. corymbiflora.

F. venusta.

F. rosea.

F. pumila × *F. alpestris* (2 *N*).

F. pumila × *F. alpestris* (2 *F*).

F. globosa × *F. gracilis* (11 *A*).

F. globosa × *F. gracilis* (11 *B*).

F. globosa × *F. Riccartoni* (10 *A*).

F. fulgens × *F. virgata.*

F. corymbiflora × "Ballet Girl."

The irregularities in the distribution of the chromosomes in the *Fuchsias* frequently leads to the sterility of the pollen grains. Tischler

(15, p. 108) has pointed out with justice that such an unequal partition of the chromatin need not necessarily lead to the sterility of the resulting pollen grains. At the same time one cannot avoid the conclusion that the fact of the existence of such an abnormal distribution is an early indication of a derangement in the mechanism of the cell and, in the *Fuchsias* at least, this may become intensified in the later stages of development so that many of the pollen grains which result become sterile. This sterility of the pollen grains has frequently (see 2) been regarded as the peculiar attribute of hybrids, but the list of *Fuchsias* which has been given above does not support this view.

Thus *F. arborescens*, which is a pure species, produces a large proportion of sterile pollen, whilst a definite cross between *F. pumila* \times *F. alpestris* exhibits quite regular pollen development, and nearly all the grains which are produced are fertile. Other instances of the same fact will be seen in the list.

A study of the species and varieties of *Fuchsia* shows quite definitely that the hybrid character is not the only determining factor in the production of sterile pollen grains.

There are a number of other instances already known in the literature which all point in the same direction. Thus Gates and Goodspeed (7) have recently described a number of interesting cases of pollen sterility in plants which are undoubtedly not hybrids. A striking instance of this is to be found in *Scoliopus Bigelovii* in which, with all possibility of crossing excluded and in their native habitat, from 3 per cent. to 32 per cent. bad pollen is produced, whilst in individual anthers the observed amount of bad pollen exceeded 45 per cent. "This in itself is a sufficient refutation of the hypothesis that bad pollen is necessarily a sign of hybridity." "Pollen sterility is rather a physiological condition which occurs in all degrees of intensity and may be due to a variety of causes" (7, pp. 3 and 4).

Dorsey (4) has also concluded that in the grapes hybridity is not necessarily the cause of sterility since both sterile and fertile hybrids occur among cultivated varieties.

Earlier references pointing to the same conclusion may be found in the literature. Thus Lidforss (9 and 10) found that the hybrid *Rubus caesius* $\sigma \times$ *Rubus acuminatus* f had a higher percentage of good pollen than one of its parents (*R. acuminatus*). Hildebrand (8) recorded the fact that whilst the hybrid *Chamaedorea Ernesti Augusti* $\text{f} \times$ *Ch. Schiedeana* σ produced mostly bad pollen, the reciprocal cross gave rise to individuals in which the pollen appeared normal.

These examples might be multiplied but sufficient has been said to show that, whilst hybridisation *may* lead to pollen sterility, this is neither the sole nor ultimate cause of this phenomenon. Any factor which upsets the harmonious interaction normally taking place between nucleus and cytoplasm may lead to the sterility of the pollen grains.

I may mention here several cases which have come to my notice.

During the summer months of 1906 and 1907 I made numerous collections of the flower buds of *Tragopogon pratensis* in order to study the development of the pollen. In all these collections, without exception, the development of the pollen grains took place in a perfectly normal manner and four pollen grains were invariably formed from each mother-cell.

Several plants were, however, grown late in the season of 1907 and anthers were examined in '6% NaCl solution upon 20th December. There had been a cool, damp autumn and the thermometer had on several occasions sunk to 25° F. It was found that under these conditions the development of pollen had become irregular and that numerous supernumerary pollen grains had been formed. In one case nine grains had been produced from one mother-cell (Fig. 28) and in others only two pollen grains were formed from the mother-cell. In some instances only a single pollen grain was produced from the mother-cell. The variation in the size of the pollen grains was very great: thus in one instance two neighbouring pollen grains within one mother-cell measured respectively 28 μ and 12 μ .

Some similar observations which I made upon *Oenothera biennis* have already been mentioned by Prof. Farmer and Miss Digby (5, p. 200) in a footnote to their paper "On the cytological features exhibited by certain varietal and hybrid ferns." Here the late season, with cold nights, was also effective in producing abnormalities in the pollen development of a plant which usually exhibits perfectly normal pollen formation.

Another interesting instance of irregular pollen development has come under my notice. It is that of *Geranium ibericum* Cav. A plant of this species has been growing in my garden for many years and during this time it has constantly failed to develop fertile pollen. I have examined a number of other plants growing at Catford and at Kew and in all these cases the stamens never developed any fertile pollen grains.

A study of the pollen development showed that the distribution of chromosomes was very irregular during meiosis, and that a varying number of pollen grains were initiated in each mother-cell.

Fig. 25 shows a case in which eight cells had been formed from one

mother-cell. The later stages of pollen development were very abnormal, and, whilst the materials for the formation of a pollen membrane were manufactured by the cytoplasm, these were only rarely laid down as a coherent wall.

In Fig. 26 two pollen grains are represented at a later stage of development. Under a very slight pressure upon the cover-glass, the cytoplasmic body, bi-nucleate in one case and tetra-nucleate in the other, emerged from the imperfectly developed membrane in the manner shown in the sketch.

Through the kindness of the authorities at the Herbarium at Kew I was able to examine several flowers of *G. ibericum* Cav. which had been brought from their native habitat in Armenia. In the stamens of all of these perfectly good pollen had developed.

Whilst working at the John Innes Horticultural Institution I examined the flowers of a plant of *G. ibericum* growing in the garden of the Institution and to my surprise I found that this developed perfectly fertile pollen grains like those found in flowers from Armenia.

The Merton plant regularly set seed and I raised a number of seedlings from it. These I planted in my garden side by side with the sterile specimen and these have regularly, year after year, produced fertile pollen and set their seed, whilst the sterile plant continued to form stamens containing only abortive pollen. The fertile and sterile plants, apart from the difference in pollen development, were identical in all respects both in their vegetative and floral characters.

These observations seem to indicate that a plant, fertile in its own homes, when brought under the changed conditions of a different country, may produce offspring some of which are identical with the parent form whilst others are sterile mutants.

The facts which have been recorded here do not support the view that irregular meiosis and non-fertile pollen are necessarily an indication of the hybrid character of the plant producing them. Cases have been quoted in which undoubted hybrids (e.g. *F. pumila* \times *F. alpestris*) developed fertile pollen, and showed no irregularities during the meiotic divisions. On the other hand it has been shown that plants which we have every reason to regard as good species, such as *Tragopogon pratensis*, may exhibit all the irregularities in pollen development which have by some been regarded as the attribute of hybrids alone. In a third case, that of *Geranium ibericum*, sterile mutants (as regards the pollen grains) appear to have been developed side by side with offspring which have remained unaltered under the influence of a changed environment.

B. *Genetics of Fuchsia.*

In this section a number of lines of investigation were commenced and a brief account of these, so far as they have at present gone, is given here.

(1) "*Faux hybrides*" in *Fuchsias*.

Certain hybrids were described in 1894 by Millardet (13 and 13 a) between various species of the genus *Vitis* in which the maternal characters were represented to the total exclusion of all those derived from the male parent. To these hybrids Millardet gave the name of "Faux hybrides." The genus *Vitis* falls into two sections—Euvitis and Muscadinia—and it was found that it was only when species belonging to different sections of the genus were crossed that "faux hybrides" appeared. Thus when varieties of *Vitis vinifera* (belonging to the section Euvitis) were pollinated by *Vitis rotundifolia* *Scuppernong* (belonging to the section Muscadinia) offspring were obtained which in all respects resembled the female parent, *Vitis vinifera*. If these seedlings were in their turn again crossed with *Vitis rotundifolia* *Scuppernong* there was still no appearance of any of the *rotundifolia* characters in the following generations, but all the seedlings entirely resembled *Vitis vinifera*.

Gard (6) found in 1903 that the resemblance between the offspring of these pollinations and their maternal parent extended even to the anatomical features. Millardet also observed that the pollination of varieties of *Vitis vinifera* with the pollen of *Ampelopsis hederacea* also yielded "faux hybrides" in which no single character of *Ampelopsis* occurred.

Another interesting case of the existence of hybrids in which the characters of one parent are alone represented is presented by the genus *Fragaria*. In this instance it is usually the male parent which predominates although the reverse is said also to occur in other crosses within the genus (Millardet 13 a).

Sohns-Laubach (14) for example found that when *Fragaria virginiana* was pollinated with pollen from *F. elatior* the offspring exactly resembled the male parent (*F. elatior*) in all their characters. "Faux hybrides" of apparently a similar nature, but in which the maternal characters predominate, have been observed in the genus *Rubus* by both Millardet and Lidforss (13 a, 9 and 10).

Among the species and varieties of *Fuchsia* several cases have been recorded in which the female parent apparently predominates over the male. Lowe (11) mentions that *Fuchsia fulgens* crossed by the variety

"Semiramide" and the reciprocal cross yielded seedlings which in both instances resembled the female. Meehan (12) recorded the occurrence of offspring resulting from the pollination of *Fuchsia arborescens* with pollen of a garden variety of *Fuchsia* in which the characters were entirely those of the female parent (*F. arborescens*). I commenced a series of observations upon this subject but these have up to the present been only partially completed. I will, however, give a brief account of these observations so far as they have gone.

After due attention to the careful castration of the flowers of a plant of *Fuchsia fulgens* these were pollinated with pollen from *F. virgata*. Twenty-eight seedlings were obtained and these entirely resembled the female parent (*F. fulgens*) and no trace of *F. virgata* could be detected in any of them.

Subsequently a further cross was made between *Fuchsia fulgens* (♀) and *F. virgata* (♂). These gave seedlings which, with one doubtful exception, all resembled *F. fulgens* in every respect.

These *F. fulgens*-like offspring were selfed and, of the 50 seedlings which were grown on, 44 plants flowered and were the exact replica of *F. fulgens* both in their flowers and their vegetative characters, whilst the six remaining plants did not flower before my observations had to be broken off, but they resembled *F. fulgens* in all their vegetative characters. Another cross was made between *F. fulgens* (♀) and the garden variety "Ballet Girl" (♂). Twelve seedlings were obtained of which five flowered before the observations were interrupted. These all resembled *F. fulgens* and showed no trace of "Ballet Girl" in any of their characters. In all cases every precaution had been taken to remove the stamens from the ♀ flowers at an early stage of their development and before there was any possibility of their dehiscence.

The reciprocal cross between *F. virgata* (♀) and *F. fulgens* (♂) was made and in this case the offspring showed characters derived from both parents. The size and the form of the leaves were intermediate between those of the two parents. The red pigmentation, which is characteristic of *F. fulgens* but absent in *F. virgata*, was very strongly marked in some of the hybrids (especially in the plant 3 *G*) and completely wanting in others (e.g. 3 *B*). In other cases it was entirely limited to the veins, which were bright red, whilst the general tissues of the leaf were pure green (e.g. 3 *F*). The flowers were in all cases closer to *F. virgata* than *F. fulgens* in their general form and colour, but in many instances showed traces of their *F. fulgens* ancestry in the slightly increased length of the calyx-tube.

The crowded arrangement of the flowers in a terminal inflorescence was in some cases very like that occurring in *F. fulgens* and altogether dissimilar to the loose, paired arrangement of the blooms in *F. virgata*. This feature was particularly well developed in the hybrid 3P and the fact that the individual blooms were all very like those of *F. virgata* made the appearance all the more striking. These hybrids showed a very wide variation in size, some being stronger growing than either of the parent forms whilst others were very diminutive. Pl. XXIV represents the two extremes in size among these seedlings. The taller plant measured 130 cm. in height, whilst the dwarf specimen was only 8 cm. high.

The late E. J. Allard, Superintendent of the gardens of the John Innes Horticultural Institution, made a cross between *Fuchsia corymbiflora* (♀) and *Fuchsia* hybrid ("Ballet Girl") (♂). The flowers of *F. corymbiflora* were castrated at an early stage and precautions were taken to prevent foreign pollen reaching the plant.

A number of seedlings were obtained which resembled the female parent in all respects and showed no trace whatsoever of the male parent "Ballet Girl." I made further crosses between these seedlings and "Ballet Girl" and obtained three fruits in one case and two from another cross, but unfortunately the work was interrupted before the seedlings from these fruits could be raised.

Meehan recorded in 1891 the fact that *Fuchsia arborescens* (♀) crossed with pollen of a garden variety of *Fuchsia* yielded offspring which solely resembled *F. arborescens* to the total exclusion of the characters of the male parent.

I made a large number of crosses between *F. arborescens* and *F. virgata* and between *F. arborescens* and *Fuchsia* hybrid ("Ballet Girl"), but none of the fruits set, probably owing to the lateness in the season when *F. arborescens* first came into flower that year.

From what has been said above it will be seen that there are certainly two instances of "faux hybrides" in the *Fuchsias*, viz., the cases of *F. fulgens* and *F. corymbiflora*. A third instance—*F. arborescens*—has been recorded, but this requires to be repeated with all the precautions which we now know to be necessary to prevent foreign pollination.

The underlying cause of the appearance of these "faux hybrides" in *Fuchsias* can only be determined by a careful cytological study of the individual cases. Several explanations are, however, possible. It may be that, as in *Caelebogyne ilicifolia*, *Euphorbia dulcis*, *Nothoscordum*

fragrans, etc., fertilisation of the egg-cell takes place and this leads to the development of an adventitious embryo, formed vegetatively, without the egg-cell itself contributing to the new generation¹.

Or, as in the case of *Opuntia vulgaris*, the embryo may arise vegetatively as the direct result of the stimulus given by the penetration of the pollen tube into the tissues of the stigma and style although fertilisation of the egg-cell is not necessarily effected at all².

A third possibility is that fertilisation of the egg-cell takes place normally, but the female nucleus alone is able to impress itself upon the cytoplasm of the egg whilst the male nucleus remains completely without influence.

Such a case is known to zoologists through the work of Godlewski upon the fertilisation of the eggs of *Echinus* with the sperm of the Crinoid *Antedon*. Here he obtained larvae which showed no trace of Crinoid character³.

It is to be hoped that future investigation may discover which of these possible explanations of the phenomenon applies in the case of the Fuchsias.

(2) *Double Fuchsia*, "*Ballet Girl*."

A plant of this was selfed and yielded a quantity of seed. From a sowing of this six seedlings were raised and grown to the flowering stage. Of these plants all six were identical and the exact likeness of the original parent. Although I have not been able to ascertain the history of "*Ballet Girl*" it cannot be doubted that it is a hybrid and it is rather unexpected to find no trace of segregation amongst its offspring.

(3) *F. globosa* (green) × *F. gracilis* (variegated).

Fuchsia globosa with green foliage was crossed with *Fuchsia gracilis* possessing variegated leaves.

Thirteen seedlings were obtained showing the following characters:—

8 seedlings with *green* cotyledons.

3 seedlings with *yellow* cotyledons.

2 seedlings with *white* cotyledons.

¹ See Strasburger, E., "Ueber Polyembryonie." *Jen. Zeitschr. f. Naturwiss.* Bd. xii. p. 662, 1878.

² See Ganong, W. F., "On polyembryony and its morphology in *Opuntia vulgaris*." *Bot. Gaz.* Vol. xxv. p. 224, 1898.

³ See Godlewski, E., "Untersuchungen über die Bastardierung der Echinoiden und Crinoiden Familien." *Arch. Entwickl. mech.* Bd. xx. p. 579, 1906.

(4) In addition to the above several other crosses were made but an insufficient number of seedlings had been obtained to make them worth while describing at any length.

(a) Crosses were made between a single form with rosy-pink petals and the double flowered "Ballet Girl" with white petals. Offspring produced flowers which had rosy-pink petals and there were numerous grades among them between completely single flowers and completely double ones.

(b) *Fuchsia procumbens* (♀) × *F. reflexa* (♂). Only a single seedling was produced from this cross. The upper branches of the plant were erect like those of *F. reflexa* whilst the lower ones were trailing like those of the female parent. The flowers were small, with pale pink sepals and a corolla reduced to a small deep pink scale. The stamens were very rudimentary and completely sterile. The pistil possessed a four-lobed stigma; the style being pink and the stigma a lighter shade of the same colour.

(c) A number of crosses were made between *F. Cottinghami* (♀) and *F. reflexa* (♂); and between *F. parviflora* (♀) and *F. reflexa* (♂). In both cases the female parent possessed completely sterile anthers whilst the male parent (*F. reflexa*) produced good, fertile pollen. The object of the cross was to test the inheritance of the fertile and sterile character of the pollen in the two parents.

Results were not carried far enough to deal with the point efficiently but one seedling was obtained from crossing *F. Cottinghami* with *F. reflexa* in which the pollen was perfectly fertile and resembled that of *F. reflexa* in possessing two interstitial bodies.

Further crosses were made between this seedling (No. 7) (♂) and *F. Cottinghami* (♀). In the offspring of this cross either all the stamens were sterile or in some cases (e.g. No. $\frac{21}{16}$) a certain amount of fertile pollen with two interstitial bodies was produced amongst a quantity of grains which were empty and bad.

The work for this paper was carried out at the John Innes Horticultural Institution and I wish to express here my most sincere thanks to Mr Bateson for the facilities which were afforded me and for the interest he has taken in the work.

EXPLANATION OF PLATES.

For Figs. 18, 25, 26, 27, and 28, an one-eighth inch objective and No. 2 compensating eye-piece were used; for all other Figs. a Zeiss 2 mm. lens of 1.40 N.A. and an 18 compensating eye-piece were employed.

PLATE XXII.

Figs. 1—13. *Fuchsia hybrid*. Stages of first meiotic division in pollen-mother-cells. $\times 2700$.

Figs. 14 and 17. *Fuchsia hybrid*. Stages of second meiotic division in pollen-mother-cells. $\times 2700$.

PLATE XXIII.

Figs. 15 and 16. *Fuchsia hybrid*. Stages of second meiotic division in pollen-mother-cells. $\times 2700$.

Fig. 18. *Fuchsia hybrid*. Ten young pollen grains all derived from one pollen-mother-cell.

Fig. 19. *Fuchsia hybrid*. Supernumerary cells all derived from one pollen-mother-cell. $\times 2700$.

Figs. 20 and 21. *Fuchsia globosa*. Telophase of first meiotic division of pollen-mother-cells. $\times 2700$.

Fig. 22. *Fuchsia globosa*. Second meiotic division; early anaphase. $\times 2700$.

Figs. 23 and 24. *Fuchsia corallina*. First meiotic division of pollen-mother-cells. $\times 2700$.

Fig. 25. *Geranium ibericum*. Eight young pollen grains all derived from one pollen-mother-cell.

Fig. 26. *Geranium ibericum*. Binucleate and tetranucleate protoplast escaping from incomplete wall on slight pressure.

Fig. 27. *Fuchsia hybrid*. Pollen grain with only a single interstitial body.

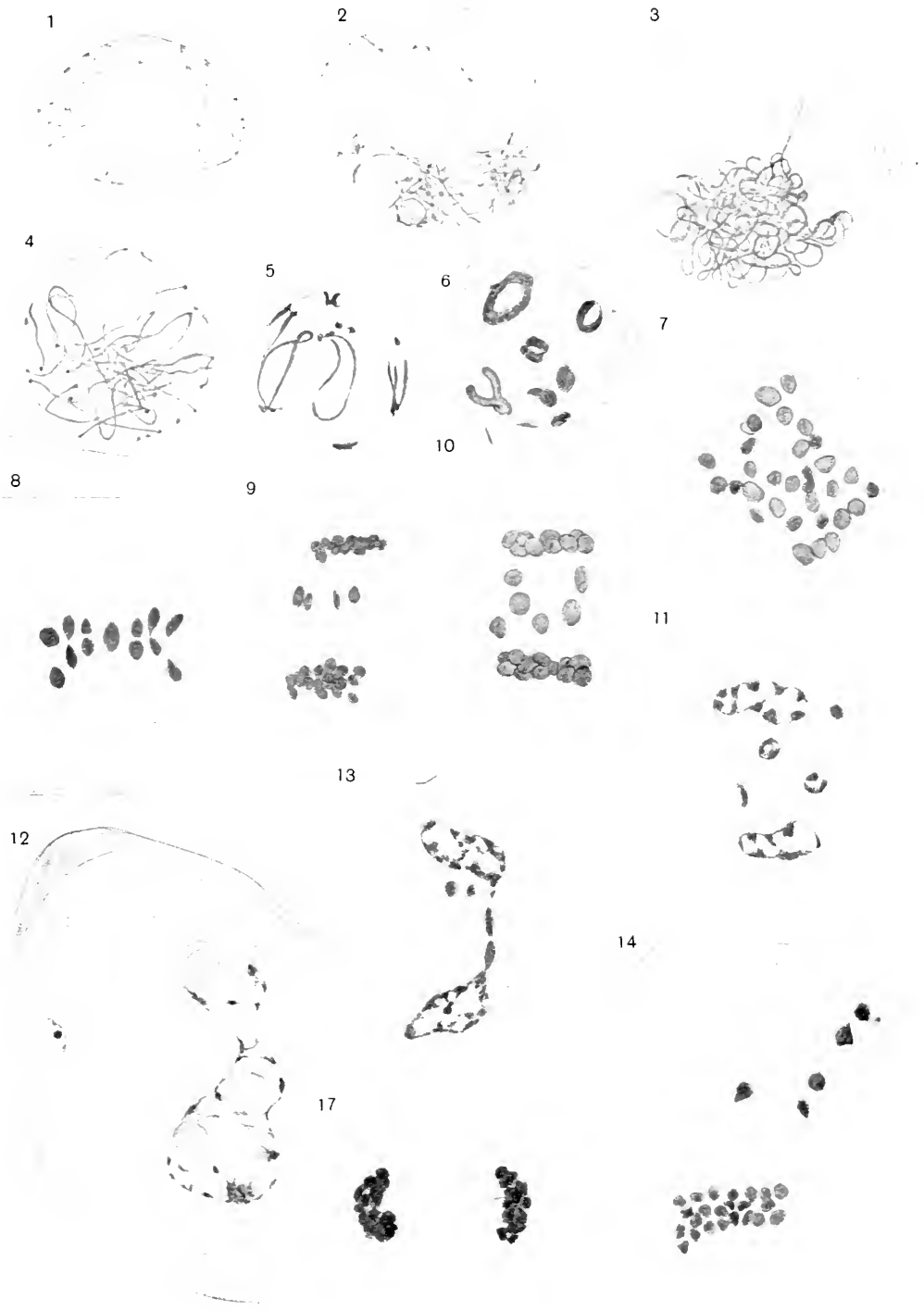
Fig. 28. *Tragopogon pratensis*. Nine pollen grains all derived from one pollen-mother-cell as a result of low temperature.

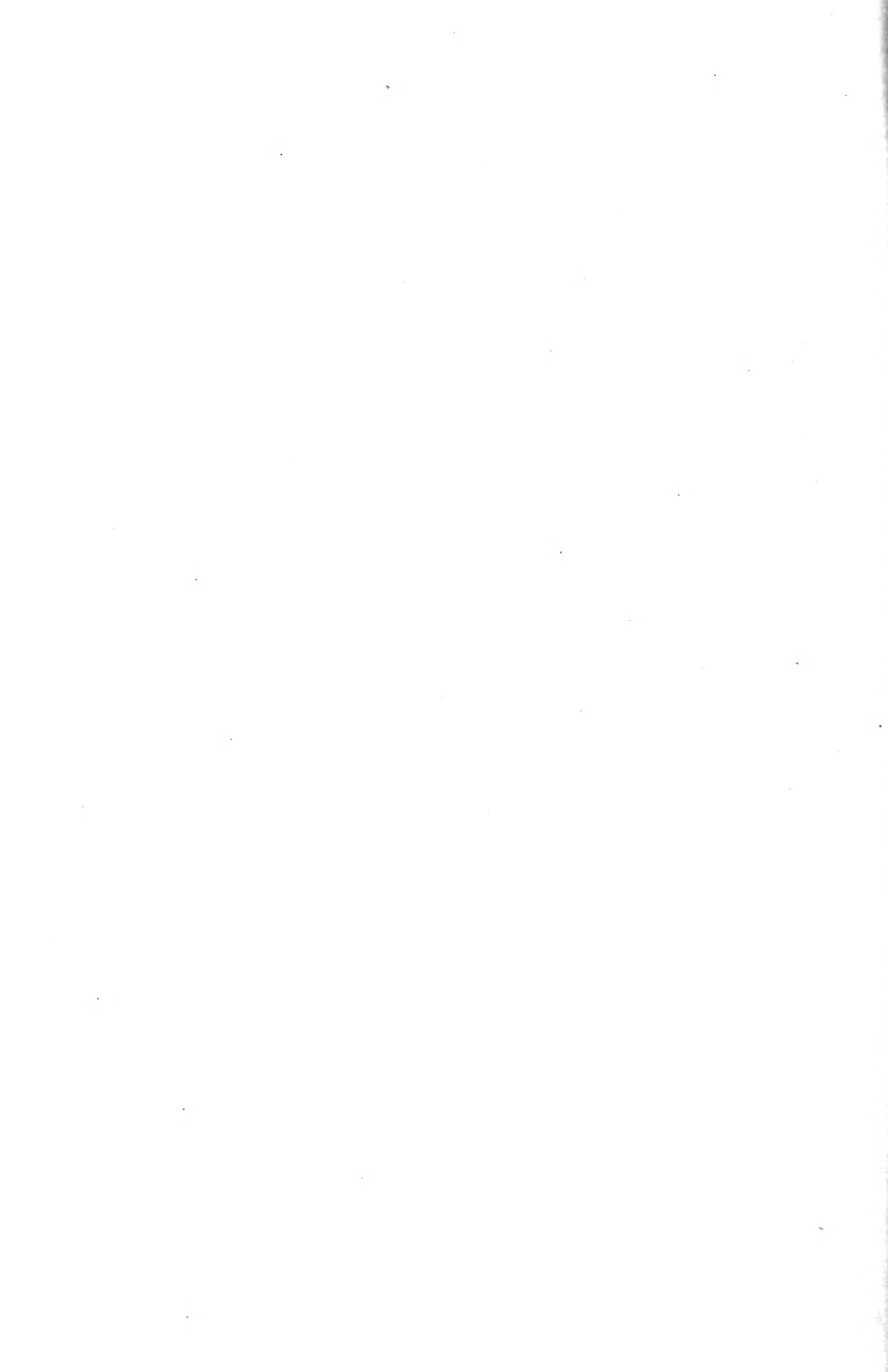
PLATE XXIV.

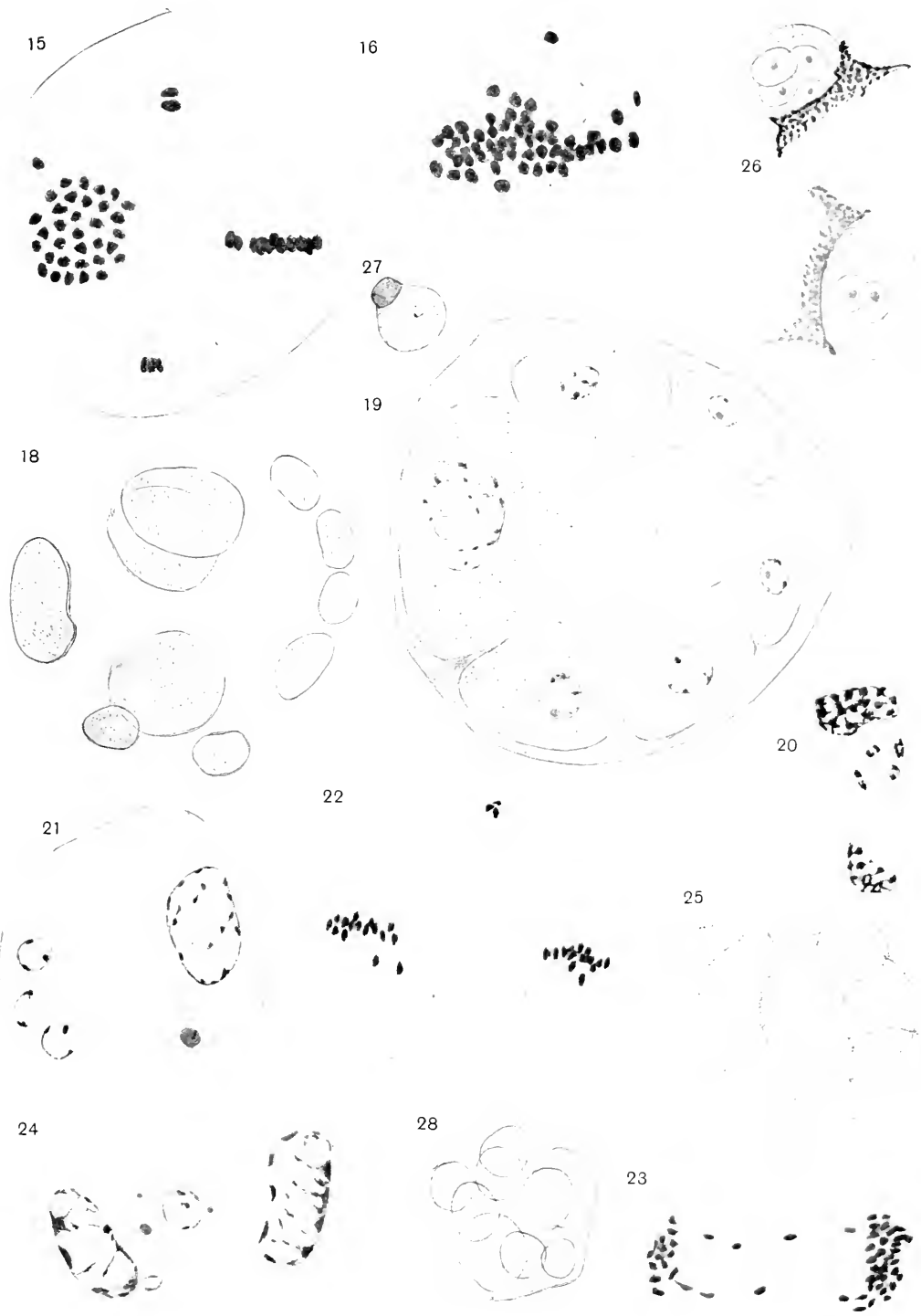
Fuchsia virgata \times *F. fulgens*. Two plants (3 R and 3 T) of F_1 .

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Fuchsia virgata \times *F. fulgens*. Two plants (3R and 3T) of F_1 .



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LINKAGE IN *GAMMARUS CHEVREUXI*.

BY J. S. HUXLEY,

New College, Oxford.

THE work of Allen and Sexton ('17) showed that Mendelian inheritance occurred in *Gammarus chevreuxi*. Three mutations in eye-colour appeared and proved to be due to recessive changes in three Mendelian genes. These factors may be designated respectively B (black) and b (red); C (colour) and c (absence of colour); and W (white) and w (no-white). However, some of the ratios obtained from crosses where two or three factor-pairs were involved departed considerably from expectation. It seemed that they might be due to linkage of factors B and C . This hypothesis could not be tested from the data in Allen and Sexton's paper, since the make-up of the heterozygotes involved was not recorded. Accordingly it was decided to test for linkage by breeding. Through the kindness of Mrs Sexton, I was provided with a number of almost mature *Gammarus* heterozygous for all three factors $\left(\frac{B, C, W}{b, c, w}\right)$ and made up by crossing the wild strain $\left(\frac{B, C, W}{B, C, W}\right)$ with triple recessives $\left(\frac{b, c, w}{b, c, w}\right)$. Unfortunately, only a very few triple recessives were available, so that the more desirable back-cross could not be undertaken at once. A number of broods, however, have been raised from the triple heterozygotes mated *inter se*, and figures obtained which warrant the assertion that linkage exists between B and C . I have therefore thought it best to publish at once the data on which this assertion is based, while continuing and amplifying the experiments in various directions.

If no linkage exists among the factors and no differential viability among the classes of offspring, the mating I have mentioned should give the following classes and proportions of offspring in F_1 :

Black, B, C, W	27
Red, b, C, W	9
Albino, $B(b), c, W$	12
Black, No-white, B, C, w	9
Red, No-white, b, C, w	3
Colourless, $B(b), c, w$	4
Total	64

There appears from Allen and Sexton's work to be very little difference in viability between the different classes. The recessives are perhaps a trifle less hardy, but the differences from expectation thus produced in the ratios are negligible. As we shall see, this factor can probably be disregarded in the experiments here recorded, since the double recessive classes, which should be the least viable of all classes, are not below expectation.

There is no possibility of confusing any classes save blacks and reds (BCW and bCW). Occasionally the heterozygous blacks show a distinctly russet or dark crimson tint. This, however, is in almost all cases wholly distinct from the light scarlet of the reds. Very rarely specimens are met with among the coloured-with-white class which are apparently intermediate; whenever this is so the fact has been noted. The doubtful cases almost all cropped up at the outset, and disappeared with practice. In the coloured no-white classes (B, C, w and b, C, w), however, I have never met with heterozygotes which could not be at once classed without hesitation; the colour stands out much more clearly when not against the chalky background of the white pigment. If there is linkage between B and C (and only between B and C) the ratio of black-with-white (B, C, W) to red-with-white (b, C, W) should be the same as that of black no-white (B, C, w) to red no-white (b, C, w). Since the former ratio is actually found to be very nearly equal to the latter, and since in this latter ratio there is no possible source of error from confusion of classes, we may assume that any error thus produced in the former ratio is negligible, an assumption further justified by the rarity of doubtful cases.

Some broods were kept at room-temperature (10° – 15° C.), others in an incubator at 25° – 26° C. Otherwise the treatment was the same for all. The figures indicate that linkage (as in *Drosophila*—see Plough, '17) is less intense at the higher temperature. There are further some slightly aberrant ratios in the no-white (ww) classes. With these subjects I do not propose to deal until I have further data; here I shall only discuss the question of linkage between B and C .

If there is linkage between B and C of such strength that p represents the linkage and $1 - p$ the crossover-value in the female, while q and $1 - q$ are the corresponding values in the male, we should expect the following ratios (see Haldane, '19):

Black + Black No-white ($B, C, W + B, C, w$).....	$2 + pq$
: Red + Red No-white [$b, C, W + b, C, w$].....	$1 - pq$
: Albino + Colourless [$B(b), c, W + B(b), c, w$]...1.	

The following table gives the data. All broods in which there was any doubt over the eye-colour of any individual have been excluded from the main table, but are given at the close for the sake of completeness.

TABLE I.

Category	Black <i>B, C, W</i>		Red <i>b, c, w</i>		Albino <i>B (b), c, W</i>		Colourless <i>B (b), c, w</i>		Totals
	<i>B, C, W</i>	No-white <i>B, C, w</i>	<i>b, c, W</i>	No-white <i>b, c, w</i>	<i>B (b), c, W</i>	<i>B (b), c, w</i>			
A. At room temperature (74 broods)	509	164	119	46	232	59			
	673		165		291				1129
B. First broods after transference from room to 25° C. (15 broods)	97	52	18	11	42	20			
	149		29		62				240
C. Subsequent broods at 25° C. (44 broods)	262	106	80	29	115	50			
	368		109		165				642
D. Total of A, B, and C (133 broods)	868	322	217	86	389	129			
	1190		303		518				2011
E. Total of (D) with all doubtful broods added (13 more broods)	943	350	255	98	426	137			
	1293		353		563				2209
F. Expectation for (D) if no linkage present	818.4	282.8	282.8	94.3	377.1	125.7			
	1131.2		377.1		502.8				2011.1

It will be seen that, while Albino + Colourless are close to expectation, the ratio of the *W* to the *w* classes, as I mentioned above, shows some peculiarities, the classes containing *ww* usually appearing slightly in excess, especially at the higher temperature. The reason for this is not yet apparent; but whatever the cause, the deviations do not support the idea of linkage of *W* with the other factors.

When we come to the ratio of blacks to reds, however, we find an excess of blacks and a deficiency of reds, both in the with-white and no-white classes. The ratios of black to red previously obtained by Allen and Sexton (*loc. cit.*, p. 343), when only the factor-pair *B, b* was involved, conformed very closely to the expected 3:1. Differential mortality may also for this reason be excluded. Since in my stock *B* came in with *C*, and *b* with *c*, we should expect to find this excess of blacks and deficiency of reds (a corresponding excess of reds and deficiency of blacks being carried by the albino and colourless classes).

Assuming that there is linkage between *B* and *C*, then let *r* be the geometric mean of the linkage values *p* and *q*. We then find that the value of *r*, as calculated from the totals in (D), is given as follows:

$$\frac{2 + pq}{1 - pq} = \frac{1190}{303} \text{ from which } r = \sqrt{pq} = .6255;$$

and $100(1 - r) (= \text{mean crossover-value}) = 37.45 \pm 0.69 \%$.

This gives a gametic ratio of almost exactly $5BC:3Bc:3bC:5bc$.

The figures for *A* (broods at room temperature only) are :

$$r = \cdot 6397; \text{ mean crossover-value} = 36\cdot 03 \pm 0\cdot 89\%.$$

Those for *C* (broods at 25° C. only) are :

$$r = \cdot 5608; \text{ mean crossover-value} = 43\cdot 92 \pm 1\cdot 28.$$

It will be seen that the difference between the crossover-values of *A* and *C* is 7·89 %. This is more than 6 times the larger probable error, and is therefore significant.

Group *B* represents the total of the broods first produced after transference from room temperature to 25° C. The eggs were already fertilized and in the pouch before transference, so that the high linkage value

$$r = \cdot 7149; \text{ mean crossover-value} = 28\cdot 51 \pm 1\cdot 49\%,$$

must be regarded as an accident.

The few animals obtained from the back-cross $\frac{B, C, W}{b, c, w} \text{ } \text{♀} \times \frac{b, c, w}{b, c, w} \text{ } \text{♂}$ corroborate these findings. They are as follows :

	<i>B, C, W</i>	<i>B, C, w</i>	<i>b, C, W</i>	<i>b, C, w</i>	<i>B (b), c, W</i>	<i>B (b), c, w</i>	Total
(6 broods)	13	14	2	10	32	27	
	27		12		49		88
Expectation	<i>p</i>		:	<i>1-p</i>	:	<i>1</i>	

These show the same deficiency of both classes of reds. (They also show the excess of individuals containing *uvw*.)

If we neglect the fact that the *c, W* and *c, w* classes are not exactly half the total, we find that $p = \frac{27}{88} = \cdot 692$, with crossover-value $30\cdot 8 \pm 4\cdot 8\%$, which, with the few broods available, is a sufficiently close approximation. It should in this connection be mentioned that different pairs vary considerably in the strength of linkage which they exhibit. It should be remarked that since the crossover-values for the back-cross are of the same order as those for the heterozygotes mated *inter se*, linkage must be of about the same intensity in the two sexes. In this *Gammarus* differs from Insects, and resembles Mammals.

The abnormal ratios in Allen and Sexton's paper may all be explained on the assumption of linkage of an intensity close to that here found. E.g. their No. 6, p. 344, 2nd mating (linkage is not involved in the first mating of this heading).

If the composition were $\frac{B, C}{b, c} \times \frac{b, c}{b, c}$, then we should expect the ratio *s*, black : 1 - *s*, red : 1, albino, where *s* = either *p* or *q*.

The figures were *BC*, 31; *bC*, 8; *B(b) c*, 34; which gives $s = \cdot 7949$, with c.o.v. = 20·51 %.

No. 7, p. 345. If the cross were $\frac{B, C}{b, c} \times \frac{b, C}{b, c}$, we should expect

1 + s , black : 2 - s , red : 1, albino.

The figures were BC , 235; bC , 169; $B(b)$ c , 144; which gives $s = .7450$, with c.o.v. = 25.5% .

(d), p. 347. If the cross were $\frac{b, C}{B, c} \times \frac{b, C}{b, c}$, we should expect

2 - s (black + black no-white) : 1 + s (red + red no-white)
: 1 (albino + colourless).

The figures were B, C , 162; b, C , 202; $B(b)$, c , 127; which gives $s = .6646$, with c.o.v. = 33.54% .

The linkage-values for the two latter sets of crosses are in close agreement with my figures; those for the first cross are a sufficient approximation in view of the small numbers.

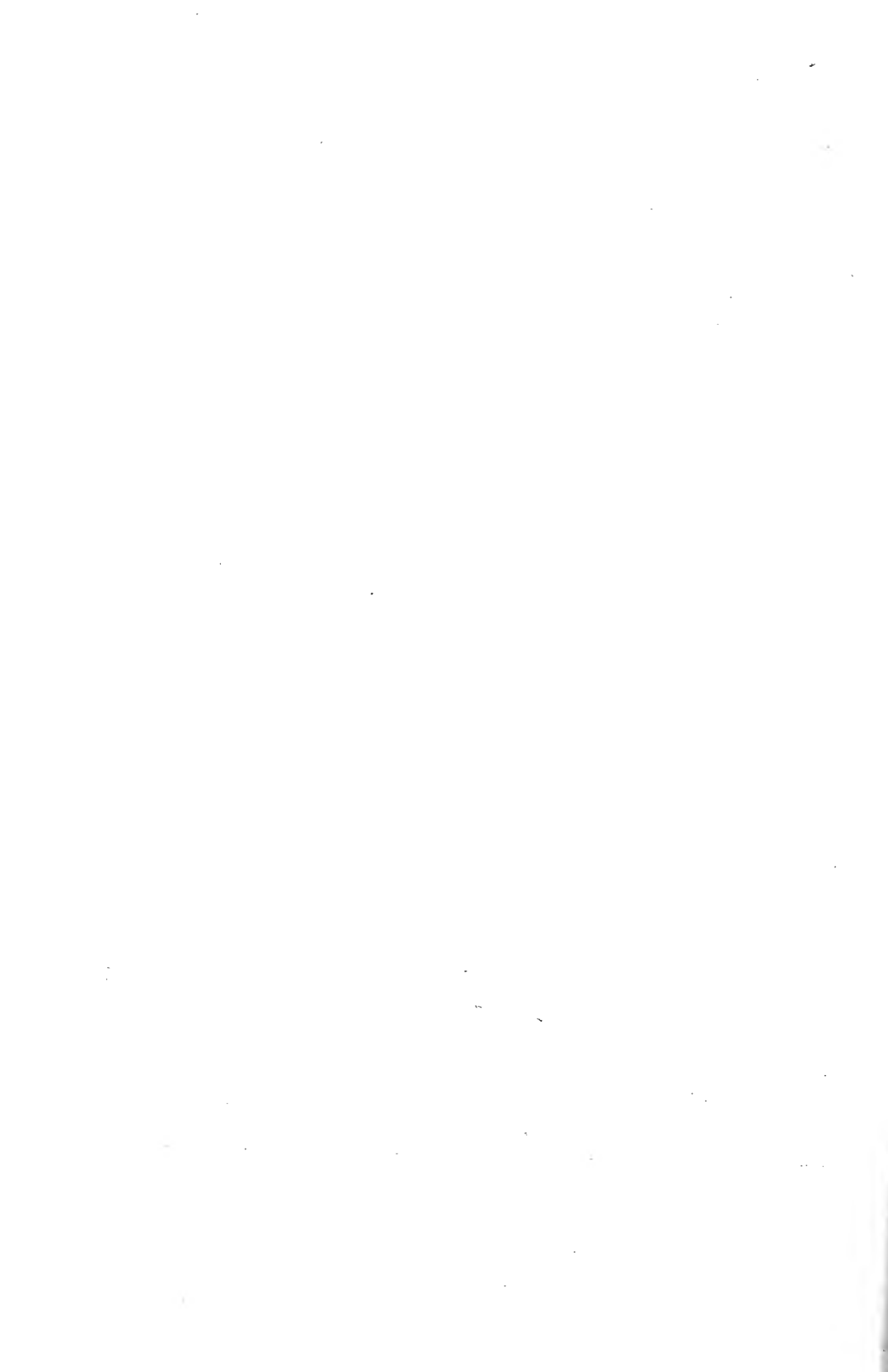
The double heterozygotes (No. 4, p. 344) and triple heterozygotes [(e), p. 347] crossed *inter se* do not show linkage ratios, presumably because the make-up was not always the same, B having sometimes entered with C , at other times with c .

The work is being continued. But the fact that this is, I believe, the first case of linkage recorded for Crustacea warrants its publication at the present stage.

In conclusion, I would like to thank Mrs Sexton of the M. B. A., Plymouth, for her kindness in providing me with material, and in placing her experience of the species at my disposal, my wife for help in caring for the animals, and Mr J. B. S. Haldane of New College, Oxford, for criticism and advice. The abnormal ratios in Allen and Sexton's paper had, I found, led Mr Haldane independently of myself to suppose that linkage might be present, but he was unable to undertake the experimental proof of the hypothesis.

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GENETIC STUDIES IN POULTRY.

IV. ON THE BARRED PLUMAGE OF CERTAIN BREEDS.

By R. C. PUNNETT, F.R.S., AND M. S. PEASE, M.A.

(With Two Text-figures.)

THE type of plumage known as barred, in which bands of different colour are arranged alternately along the feather at right angles to its main axis (cf. Fig. 1, p. 239), is characteristic of several breeds of poultry. It is to be found in its most marked form among Plymouth Rocks, Pencilled Hamburgs and Campines. Probably also the feather patterns designated as laced, pencilled¹, and spangled are intimately connected with the barred. We have long felt that a genetic analysis of barring in Poultry, with its peculiar rhythmical alternation of pigment deposition in the feather, might help to throw some light upon the problems of growth, and with this end in view we have recently commenced a series of breeding experiments. Though the work is as yet but in its initial stages, the present season has yielded a result of sufficient interest to place on record. Before doing so however we would dwell briefly upon what is known as to the genetic behaviour of barring in poultry.

In the present state of our knowledge it would appear that the barring found in Plymouth Rocks, Scots Greys and Dumpies is genetically distinct from that found in the barred breeds of Hamburgs, and in Campines. In the Rock group the birds are of the same fundamental colour throughout, and the barring effect is produced through full and faint development of this fundamental colour in alternate bands. In the Barred Rock itself, for example, the darker bands appear as grey-black, while in the lighter bands the grey colour is very faint, so that these bands appear almost, though not quite white.

¹ The use of this term in the Fancy is apt to confuse the uninstructed. The "Pencilled" Hamburg is a barred bird. We propose, for purposes of this investigation, to restrict the term "pencilled" to the characteristic pattern of the feathers in the "Partridge" varieties of Cochins, Wyandottes, etc. The connection between pencilled and barred is a close one, for feathers that would pass for barred, as well as the distinctive pencilled feathers, and intermediate types, are to be found on the same bird.

Thanks to the work of Spillman, Morgan, Pearl and others in America we realise that the barring depends upon a definite sex-linked factor acting upon a black basis. The factor would appear to be of an inhibitory nature, preventing the deposition of black pigment almost completely in the lighter bands of the feathers, slightly so in the darker ones. The action of the barring factor is also evident upon a brown basis, though not so clearly. Some years ago we made a cross between Plymouth Rock ♀ and Brown Leghorn ♂. The F_1 ♂♂ were barred like the Rock, while the F_1 ♀♀ were full black or nearly so. In the F_2 generation appeared more or less typical barred and blacks of both sexes, together with browns of various kinds (including silver-greys¹), both barred and unbarred. In these barred browns the barring was not nearly so sharp as in the barred birds belonging to the black class. For the present we are disposed to consider that the barring factor acts more intensely upon the black pigment than upon the golden pigment, if indeed it acts upon the latter at all. On this view the blurred nature of the barred browns would be due to the inhibition of only the black pigment scattered about among the gold in the mixture which goes to make up the brown bird. We realise that this can be no more than a plausible suggestion in our present state of ignorance of the pigments of the fowl's plumage. The point however deserves further investigation.

As shewn by its behaviour towards black, the barring of the Ham-burgh-Campine group is evidently different in its nature, though the only direct evidence we know of is provided by some experiments carried out a few years ago at Cambridge². In those experiments a cross was made between a Gold Pencilled Ham-burgh ♂ and a Black Langshan ♀. The F_1 birds were black (with some gold in the hackles of the cocks), and in F_2 some barred birds reappeared. The barring of the Ham-burgh is evidently recessive to self colour in this case. But it does not necessarily disappear completely on crossing. This year we mated a Gold Campine ♀ with a Barred Rock ♂ which was heterozygous in barring. The cross resulted in approximately equal numbers of barred birds very like Plymouth Rocks in plumage, and of birds wholly or predominantly black. Certain of these last however shewed coarse silver barring in some feathers, notably on the breast. This barring we suppose to have been

¹ Evidently the silver factor was carried by the Plymouth Rock ♂. Of some birds we bred this year, ex Gold Campine ♀ × Plymouth Rock ♂ (heterozygous in barring), the non-barred ones which were not full black all showed some silver markings. Here again the Rock evidently carried silver. It seems not improbable that the silver factor may be an ingredient essential to the barred pattern of the Rock Group.

² Cf. Punnett and Bailey, *Journal of Genetics*, 1918 and 1920.

derived from the Campine, and it suggests that barring is not always completely recessive to self colour. We should add that the data we have accumulated afford no evidence for supposing that the Hamburgh-Campine barring is in any way sex-linked.

We must suppose therefore that there are at any rate two forms of barring in poultry, of which one is sex-linked and dominant to self colour, while the other is more or less recessive to self colour, and does not exhibit sex-linkage. The position appeared to us so curious that we have started a series of experiments to try and determine whether there is any relation between these two groups of barring, and if so, what that relation is. For, on the face of it, it seems unlikely that a peculiar and rhythmical pattern such as barring should be brought about in two entirely independent ways. It is obvious that the most direct way of attacking the problem is to cross birds of the Rock type with those of the Hamburgh-Campine type, and to carry out an ordinary genetic analysis. This we have already commenced, but it must be several years before we can hope to complete our analysis. At the same time we have been investigating the inter-relation of the different forms of barring in the Campine itself, and it is with a result obtained here that the present note is concerned.

The barred breeds of both Hamburghs and Campines are well known in their gold and silver varieties, and a description of these will be found in any work dealing with the breeds of poultry. In the former the alternating bars are black and gold; in the latter black and white. Recently, through the enterprise of the Rev. E. Lewis Jones, the recognised authority on Campines, a third barred form has been introduced. This is the "Chamois" Campine, in which the alternating bars are white and gold¹. The relation between the Gold and the Silver Campine is that which exists between the corresponding gold and silver forms of other varieties. Silver is dominant to gold, and is sex-linked. This we proved some years ago for the gold and silver-pencilled Hamburghs, and our more recent experiments shew it to be true also for the Campines. The white bars in the Silver Campine correspond with the gold bars in the Gold Campine, and the black bars in the one to the black bars in the other. The point then arises as to the correspondence of the white and gold bars of the Chamois with the black and gold of the gold, and the black and white of the silver. In order to decide this we made the following crosses during the past season.

¹ Through the kindness of Mr Lewis Jones we obtained a few of these birds for experiment, and for this we wish to express our sincere thanks.

(1) Chamois ♂ × Brown Leghorn ♀. The seven chicks hatched from this mating were all light in down with a slight buffish tinge. The result accords with the view that Chamois acts as a dominant white, and that the cock used was homozygous in this respect. Of the seven chicks one only was reared, and proved to be a white cockerel with a good deal of gold irregularly distributed over its plumage. Here and there slight indications of barring were present.

(2) Chamois ♀ × Gold Campine ♂. Of 21 chicks produced 14 proved to be chamois, and the remaining seven gold barred. Both sexes appeared in each colour class. From this, and from other evidence, we regard chamois as dominant to gold barred, the chamois ♀ used here being heterozygous.

(3) Chamois ♀ × Silver Campine ♂. In this experiment the same chamois ♀ was used as in (2). As to be expected she gave chicks with light and with coloured downs in approximately equal numbers, viz. 17 light and 15 dark. Of the chicks with dark down those reared (1 ♂ and 3 ♀) all developed into silver barred birds. Four also of the chicks with light down were reared. All proved to be males, and all developed into *white* birds.

(4) Chamois ♂ × Silver Campine ♀. The cock here was the same bird as that used in (1), and it was to be expected therefore that all of the chicks would be light in the down. Such was the case. But although the downs were all light they fell into two distinct classes, viz. those which were light with a slight buffish tinge, and those which were mottled with buff. Of the 24 chicks hatched 12 belonged to each class. Three of those with buff mottled down¹ were reared and turned out to be all pullets, while the eight with light down reared all developed into white cockerels.

These last two experiments shew that it is possible to produce white birds from a cross between two coloured varieties, each of which breeds true to its own colour. Corresponding feathers from a Silver Campine (*a*), a Chamois (*c*), and a white (*b*) resulting from a cross between the two are shewn in Fig. 1.

We offer the following interpretation. The silver differs from the gold in the possession of a factor which inhibits the production of the gold pigment without affecting the black. This factor is sex-linked in its mode of transmission. The Chamois differs from the gold in the possession of a factor which inhibits the production of the dark melanic pigment, but appears to have little or no influence on the gold pigment.

¹ This is the down characteristic of the Chamois Campine.

When both of these inhibitors are present they lead to the formation of a white bird. Such a condition arises when a silver ♂ is mated with a chamois ♀. Assuming both parents to be homozygous it is clear that all of the offspring would be heterozygous for each of the inhibitors, and would consequently all be white. We have not actually realised a cross in which *all* the offspring were white. In Exp. (3) about half of the offspring were coloured, but this, as we have already pointed out, we regard as due to the accident of our chamois ♀ having been heterozygous for the inhibitor of melanic pigment. The chamois ♂ used in Exp. (4) was however homozygous, and all of the progeny lacked melanic

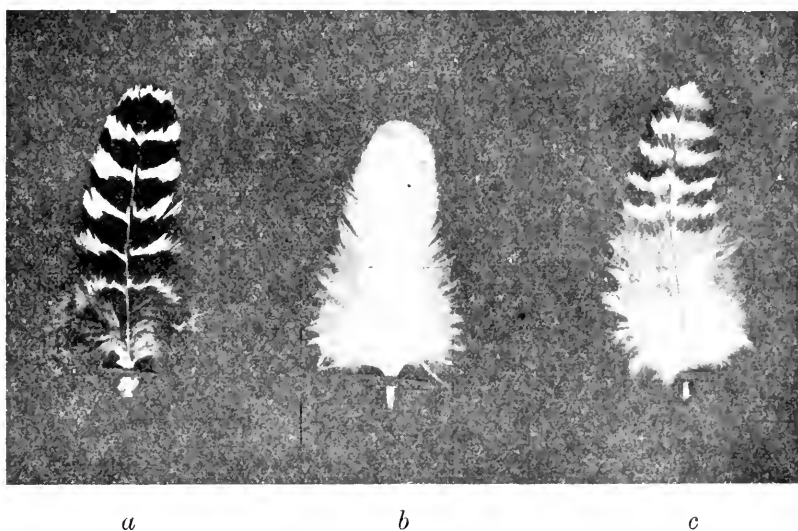


Fig. 1.

pigment except for occasional ticks. But owing to the fact that the silver ♀ is heterozygous for the gold inhibitor the ♂♂ alone from this cross are white, the pullets being chamois.

Here we may mention a point of some interest which has arisen in connection with our whites. Though at first fully white, except for a few dark ticks, they shew indications of very faint barring as they grow older. We have observed this in all of the whites we have bred—which, of course, were all heterozygous—though the barring is rather more distinct in some than in others. Mr Lewis Jones tells us that he has also observed this “ghost” barring in birds similarly bred by him, and he kindly sent us several to compare with our own. Whether the “ghost” barring is peculiar to the later feathers, or whether the feather is at first white and subsequently develops the barring on exposure to the

air, is a point we have not yet determined. We are inclined to attribute the appearance of the ghost barring to the bird's being heterozygous for the inhibitor of melanic pigment. It is certain that the ghost bars occupy the position of the black bars in a gold or a silver barred bird. For a white bird sometimes puts up a feather which is silver barred, and occasionally the silver barring is confined to one side of the rachis. In such cases the ghost bars are continuous with the black bars across the feather.

Whether the ghost barring is a heterozygous character we hope to determine next season by breeding from these heterozygous whites, and in order to make our view clear we may indicate what we expect to be the composition of the F_2 generation. Denoting the factor for the inhibitor of gold pigment by **S**, and that for the inhibitor of melanic pigment by **X**, we suppose the genetic constitution of the F_1 birds to be **SsXx**. The gametes of the F_1 ♂ should therefore be **SX**, **Sx**, **sX**, **sx**. Since **S** is sex-linked the female-producing gametes of the F_1 ♀ will be **sX** and **sx**, while the male-producing will be **SX** and **Sx**. The nature of the F_2 generation to be expected is indicated in Fig. 2.

SX SX Full white	SX Sx Ghost-barred	SX sX Full white	SX sx Ghost-barred	} males
Sx SX Ghost-barred	Sx Sx Silver-barred	Sx sX Ghost-barred	Sx sx Silver-barred	
sX SX Full white	sX Sx Ghost-barred	sX sX Chamois	sX sx Chamois	} females
sx SX Ghost-barred	sx Sx Silver-barred	sx sX Chamois	sx sx Gold-barred	

Fig. 2.

Five different kinds of birds are to be looked for on this hypothesis, though, as shewn in the appended table, the distribution of these between the sexes should be very different.

	Males	Females	Totals
Full white ...	2	1	3
Ghost-barred ...	4	2	6
Chamois ...	—	3	3
Silver-barred ...	2	1	3
Gold-barred ...	—	1	1

Further work however must shew whether this is the correct interpretation.

A STUDY OF THE VARIATION IN SEEDLINGS OF THE WILD HOP (*HUMULUS LUPULUS* L.).

BY E. S. SALMON AND H. WORMALD.

(Research Department, S.E. Agric. College, Wye, Kent.)

(With Plate XXV.)

IN 1913 it was decided to investigate whether seedlings of the wild hop showed any resistance to the attack of the mildew *Sphaerotheca Humuli* (DC.) Burr., and if so, whether this resistance was correlated with any morphological character.

It was necessary therefore to obtain seed of the wild hop. *H. Lupulus* is indigenous in Southern, Northern and Mid-Europe and in Northern and Mid-Asia¹. Hooker (*Students' Flora*) and Babington (*Manual of British Botany*) describe the plant as a true native in the South of England. The so-called "wild hop," however, found growing commonly in hedges in counties such as Kent and Sussex where commercial hop-growing is practised, is either an "escape" and belongs to some commercial cultivated variety, or possibly may be a "cross" between the wild hop and some cultivated variety. Similarly in those countries on the Continent where hops are cultivated, e.g. Germany, France, Russia, etc., the same uncertainty may exist as to the true *status* of a hop growing apparently wild². At the commencement of our investigations we believed it to be a fact that the hop had never been cultivated in Italy, and we procured, through the courtesy of Prof. P. A. Saccardo, seed of the wild hop, collected by him and labelled "Vittorio (Treviso), ad sepes, omnino sponte, Oct. 1913." Subsequently a doubt arose in our minds as to the certainty of this seed having originated solely from the wild plant.

¹ The wild hop of North America is, we consider, a distinct species, viz. *H. Americanus* Nutt. (1)*.

² In an article by J. Schmidt entitled "The occurrence of the wild hop in Denmark" (*C. r. trav. Labor. Carlsberg*, Vol. xi. 314—329 (1917)) the author states: By "wild" is here understood "not cultivated." The forms studied by Schmidt cannot be regarded therefore as the undoubted offspring of the truly wild species.

* These numbers refer to the bibliography given at p. 267.

In 1915 we were informed by Dr M. Corvi, of the R. Istituto Superiore Agrario of Perugia, that in the years 1860-70 the hop was cultivated near Bologna "with good results," and that experiments with its culture were being conducted in Umbria. Further, we found that although all the authors of Italian "*Floras*" give the hop the *status* of a wild plant, one of them, Parlatore (*Flora Italiana*, iv. 303 (1867)) remarks: "Il Luppolo è coltivato in alcune parti d'Italia, come a Forlì ed altrove. Tali coltivazioni sono però ancora molto ristrette tra noi, facendosi venire il Luppolo stesso dalla Germania." The following information, however, supplied by Prof. P. A. Saccardo in April 1916, makes it practically certain that the parent plant of the seedlings described below was the wild species. "Après investigations chez mes collègues Mittirollo, Peglion, Béguinot, etc. je peux vous assurer, *l'houblon n'a été jamais cultivé dans la province de Treviso d'où je vous l'ai expédié et où il se trouve sauvage partout abondamment, surtout sur les haies*. M. le prof. Peglion qui va publier dans ce moment un *Monografia del luppolo in Italia* m'écrit de Bologna que en toute Italie on cultive: 3 hectares de houblon dans la plaine d'Orvieto et dans l'haute-plaine de Alfina (Ombria), $\frac{1}{2}$ hectare à Pedavena (Feltre). Comme vous le voyez vous pouvez être sûr, très sûr, que les exemples que je vous ai expédiés sont absolument *spontanés et sauvages*."

The seedling plants have been raised and grown in the following manner. The bulk of the seed from Italy was sown in seed-boxes in the greenhouse in 1914 and 1915. Some of the seed germinated the same year it was sown and some in the second and even the third year after sowing. Portions of the same seed (collected in 1913) were retained and sown in 1916 and also in 1917; germination was poor and only a few seedlings were raised from these later sowings. As soon as each seedling was old enough to transplant, it was placed in a pot and kept in the (unheated and well-ventilated) greenhouse during its first year and sometimes during its second year. The 1- and 2-year old seedlings reached a height of from three to five feet. During the winter they were planted out, in blocks of 50 or more, distributed through the Experimental Hop-garden of $2\frac{3}{4}$ acres at Wye College, Kent. The seedlings were planted 3 ft. 6 in. apart in the row, and the rows were 6 ft. 6 in. apart. The plants have been given the treatment usual in a commercial hop-garden; the underground rhizome is "cut" or "dressed", each winter—an operation which removes the living, swollen bases ("strap cuts") of the annual shoots, so that the next year's shoots arise from buds lower down on the rhizome; each spring the superfluous

stems ("bines") are pulled off from the rootstock, and the remaining 2—3 stems¹ are "trained" up the "strings" (of coir yarn), for the first 4½ feet vertically to a lower wire, then at an angle of approximately 45° to a top wire 11 ft. 6 in. from the ground supported on poles². The soil was uniformly and fairly heavily manured and good cultivation was given to the whole hop-garden.

The hop plant, *Humulus Lupulus* L. is a dioecious perennial with a persistent underground rootstock from which develop long annual climbing shoots. The main axis of a shoot (or "bine") bears decussate leaves from the axils of which develop the primary branches ("laterals"). The lower laterals are usually barren but the rest form much-branched panicleate inflorescences. The rootstock of the seedling plant during its first year is very small and the shoots comparatively weak and the plant does not attain to full vigour for several years. Observations regarding morphological characters were therefore not taken until the plants were in their third year and even then some characters, particularly those depending upon vigour, e.g. length of the laterals, could not be regarded as constant.

As the plants approached an age when the various organs assumed the characters shown by the mature plant it was seen that there were marked differences in certain morphological and physiological characters. That some at least of these differences were not mere fluctuations due to environmental conditions was shown by keeping the plants under observation for several successive years and noting which characters remained constant (or fluctuated within comparatively narrow limits) for the individual plants.

The plants were first critically examined in 1916 and the characters noted of those plants which were old enough for the purpose³. Many of the plants have thus been under observation during five seasons, the rest during from two to four seasons.

The variations which have been observed are concerned with the following points:

¹ In a few cases the seedlings were planted 6 feet 6 inches apart in the row, and 6 stems trained up the strings.

² The system of wire work used in the Hop-garden is that known as the "Butcher." It has been described by A. Amos in the *Journ. Board Agric.* Vol. xvi. p. 890 (1910), where a detailed account is given of the English method of cultivating hops.

³ The variation shown by a number of male hop plants growing in the Experimental Hop-garden at Wye College and known, or believed, to be derived from seeds of cultivated hops, has already been recorded (2). The methods of observation and description adopted in that instance have been applied (modified and extended where necessary) in describing the plants noted in the present paper.

- (1) Time of flowering.
- (2) Colour of the "bine."
- (3) Relative number of glands on the leaves.
- (4) Shape of the leaves.
- (5) Colour of the leaves.
- (6) Length of the primary branches (laterals).
- (7) Characters associated with the reproductive organs, i.e. (a) in the ♂ plant, the number of glands on the perianth-lobes, on the anthers and on the receptacle; (b) in the ♀ plant, the characters of the strobile (hop-"cone"), viz. size, shape, aroma, "condition," and colour of the main axis ("strig").
- (8) Degree of susceptibility to the mildew *Sphaerotheca Humuli*, under greenhouse conditions and also in the open.

(1) *Time of Flowering.*

The great majority of the plants were much later in coming into flower than the cultivated varieties. It was found however that they showed considerable variation amongst themselves with respect to their time of flowering and particularly was this noticeable in the case of the ♂ plants; the earliest of these, as a rule, came into flower four weeks or more before the latest and this difference is maintained from year to year. By the "time of flowering" is here meant the first day on which flowers actually opened to show the stamens, in the case of the ♂ plants, and the date of the first appearance of a well developed "brush" (condition of the young "cone" when the stigmas emerge from between the bracteoles) in the ♀ plants.

The fluctuation from year to year shown by certain male plants during from three to five consecutive seasons is shown in the Table below:

Time of Flowering of certain Male Plants.

	Reference number of seedling	1916	1917	1918	1919	1920
Very early	Z 17	—	Aug. 1	July 18	July 31	July 17
"	Z 42	—	July 30	July 24	July 29	July 19
"	OG 4	—	—	July 21	July 22	July 15
Early	Z 55	Aug. 9	Aug. 1	Aug. 7	Aug. 4	Aug. 10
"	OY 23	—	—	Aug. 4	Aug. 1	Aug. 15
"	BB 35	—	—	Aug. 7	Aug. 3	Aug. 7
Midseason	OA 4	Aug. 14	Aug. 20	Aug. 15	Aug. 7	Aug. 18
"	OA 30	Aug. 18	Aug. 19	Aug. 19	Aug. 14	Aug. 20
"	OD 27	—	Aug. 24	Aug. 15	Aug. 14	Aug. 18
Late	O 15	—	—	Aug. 31	Aug. 28	Sept. 8
"	BB 23	—	—	Aug. 29	Aug. 27	Sept. 7
"	II 41	—	—	Aug. 30	Aug. 28	Sept. 4

It will be seen that, in general, the period covered by the "time of flowering" of the plants collectively is from the end of July to the beginning of September. The Table shows too that the seasonal fluctuations exhibited by the individual seedlings do not disguise the fact that certain plants can be characterized as "early," "midseason" or "late" forms. These terms do not denote distinct divisions but they may be used for convenience in placing representative types which are connected by other forms, the whole constituting a series in gradual sequence from the typically "early" to the typically "late" plants. The three plants at the head of the Table, however, appear to form a distinct class as compared with the rest of the plants which came under our purview; not only have they been consistently early flowering, but, as will be shown later, they have other characters in common.

The influence of the weather on the time of flowering is brought out in the dates under 1920. The abnormally warm weather during the early part of the growing season induced the "very early" plants to come into flower even earlier than usual, but, owing to comparatively low temperatures which subsequently obtained, the flowering of the rest was delayed and this made them later than in previous years.

The female plants were collectively later than the male plants, the earliest of them, even in favourable years, did not show the "brush" before the middle of August. It was found too that the range of variation in their time of flowering was less notwithstanding the fact that the female plants which came under observation were more numerous than the male plants¹; nevertheless plants could be distinguished which were invariably earlier or later than the average as shown in the Table below:

Time of Flowering of certain Female Plants².

	Reference number of seedling	1916	1917	1918	1919	1920
Early	OD 20	Aug. 21	Aug. 23	Aug. 21	Aug. 18	Aug. 21
"	OY 47	—	—	Aug. 20	Aug. 18	Aug. 30
"	FF 16	—	—	Aug. 22	Aug. 20	Aug. 30
Midseason	Z 19	Aug. 31	Aug. 29	Aug. 29	Aug. 22	Sept. 5
"	Z 47	Aug. 28	Aug. 29	Aug. 27	Aug. 23	Sept. 4
"	Z 58	Sept. 4	Aug. 29	Aug. 22	Aug. 23	Sept. 5
Late	HH 24	—	—	Sept. 9	Sept. 7	Sept. 15
"	OB 24	Sept. 7	Sept. 3	Sept. 1	Sept. 4	Sept. 16
"	OG 39	—	—	Sept. 6	Sept. 5	Sept. 20

¹ The number of the ♀ seedlings was 238, of the ♂ 157.

² It is to be noted, particularly with regard to the ♀ plants, that the terms "early," "midseason" and "late" as used in this paper are employed for comparing the wild hop seedling plants among themselves and do not indicate their time of flowering relative to the varieties of the hop under cultivation.

The whole period throughout which plants in flower could be found extended from the middle of July to the middle of September. For comparison with this, the time of flowering of the wild hop in Italy, as given by various Italian "*Floras*," may be noted: Comolli (*Flora Comense*, VII. 216 (1857)) "June and July"; Moricand (*Fl. Veneta*, I. 425) "July"; Naccari (*Fl. Veneta*, v. 66 (1828)) "July and August"; Parlatore (*Fl. Italiana*, IV. 303 (1867)) "June to September." It appears probable from the statement of the last-named author that early- and late-flowering forms occur wild in Italy.

(2) Colour of the Bines.

The colour of the bines (axes of the annual shoots growing from the perennial rootstock) varies from pale green to dark purplish red. The intermediate forms usually show a distinct mottling consisting of small red and green blotches, and even in the extreme forms faint indications of this mottling can often be detected. Thus in the plants with dark red bines close observation will show spots which are less dark than the prevailing colour while the green bines may show traces of pale reddish spots. The ridges on the mottled bines are often dark red giving the appearance of longitudinal dark stripes.

The difference in colour between the extreme types (green bines and red bines), and even between these and the strictly intermediate (mottled) forms, is very pronounced and as there is comparatively slight fluctuation from year to year in the colour of the bines of individual plants this character is one which strikingly illustrates the variation which obtains in the seedling hop plants.

The method of recording these colour differences was as follows:

G pale green.

G(r) pale green with faint reddish spots.

Gr green predominating but reddish spots evident.

g and *r* distinct red and green blotches giving a mottled appearance.

Rg red predominating, greenish spots present.

R(g) dark red with greenish spots hardly distinguishable.

R dark red.

The records of typical plants are given below:

Plants with green bines appear to be of comparatively rare occurrence among seedlings of the wild hop. Of the plants examined (395 in number) only three, OG 4, Z 17, Z 42 (the three plants which proved to be "very early" in flowering) can be strictly placed in this division, with the pos-

Classified as green, mottled or red bines	Reference number of seedling	Male or Female	1916	1917	1918	1919	1920
Green ...	OG 4	♂	—	<i>G</i>	<i>G</i>	<i>G</i> (<i>r</i>)	<i>G</i> (<i>r</i>)
" ...	Z 17	♂	—	<i>G</i> (<i>r</i>)	<i>G</i> (<i>r</i>)	<i>G</i> (<i>r</i>)	<i>G</i> (<i>r</i>)
" ...	Z 42	♂	—	<i>Gr</i>	<i>G</i> (<i>r</i>)	<i>G</i> (<i>r</i>)	<i>Gr</i>
Mottled ..	OA 13	♂	—	<i>Gr</i>	<i>g</i> and <i>r</i>	<i>g</i> and <i>r</i>	<i>g</i> and <i>r</i>
" ...	OA 4	♂	<i>g</i> and <i>r</i>	<i>g</i> and <i>r</i>	<i>g</i> and <i>r</i>	<i>g</i> and <i>r</i>	<i>g</i> and <i>r</i>
" ...	OG 28	♂	—	—	<i>g</i> and <i>r</i>	<i>g</i> and <i>r</i>	<i>g</i> and <i>r</i>
" ...	Z 47	♀	<i>g</i> and <i>r</i>	<i>g</i> and <i>r</i>	<i>Rg</i>	<i>g</i> and <i>r</i>	<i>g</i> and <i>r</i>
Red ...	Z 14	♂	<i>Rg</i>	<i>Rg</i>	<i>Rg</i>	<i>Rg</i>	<i>Rg</i>
" ...	Z 24	♀	<i>Rg</i>	<i>Rg</i>	<i>Rg</i>	<i>Rg</i>	<i>Rg</i>
" ...	OA 28	♂	<i>R</i> (<i>g</i>)	<i>R</i> (<i>g</i>)	<i>Rg</i>	<i>R</i> (<i>g</i>)	<i>Rg</i>
" ...	OA 16	♀	<i>Rg</i>	<i>Rg</i>	<i>R</i> (<i>g</i>)	<i>R</i> (<i>g</i>)	<i>Rg</i>
" ...	Z 49	♂	<i>R</i> (<i>g</i>)	<i>R</i> (<i>g</i>)	<i>R</i> (<i>g</i>)	<i>R</i> (<i>g</i>)	<i>R</i> (<i>g</i>)
" ...	OA 19	♀	<i>R</i> (<i>g</i>)	<i>R</i> (<i>g</i>)	<i>R</i> (<i>g</i>)	<i>R</i> (<i>g</i>)	<i>R</i> (<i>g</i>)
" ...	OF 28	♀	—	—	<i>R</i>	<i>R</i>	<i>R</i>

sible exception of one plant, II 35 (♀) which was under observation for two seasons only when it became diseased and had to be destroyed; the records for II 35 during those two years were *Gr* (1918), *Gr* (1919). Another plant which approaches the "green" bine forms is W 49 (♂), which from 1918 to 1920 was recorded as *g* and *r* (1918), *Gr* (1919), *g* and *r* (1920), and which therefore on the whole finds its place with the "mottled" plants.

Plants with red bines are by far the most numerous; in typical examples the colour is recorded as consistently *Rg*, *R* (*g*) or *R*, or as fluctuating from *Rg* to *R* (*g*)¹. One plant, OF 28, is an extreme type which produces very dark, purplish red bines distinguishing it from all the other plants in the garden.

The colour of the petioles is correlated with that of the bines; the upper surface is usually reddish and darker than the lower side, the red colour being the more deeply defined on the plants with red bines. Summarized, the distribution of the red colour with respect to the colour of the bine is as follows:

Colour of bine		Colour of petiole	
		Upper surface	Lower surface
<i>G</i> and <i>G</i> (<i>r</i>)	...	Green, but rather darker than lower surface	Green
<i>Gr</i>	...	Green, tinged with red	Green
<i>g</i> and <i>r</i> (mottled)	...	Red, tinged with green	Green
<i>Rg</i>	...	Red	Green
<i>R</i> (<i>g</i>) and <i>R</i>	...	Red	Green at distal end shading off to red at proximal end

¹ Parlatore (*Flora Italiana*, Vol. iv. 303 (1867)) writes, in his description of *H. lupulus* "Il fusto è...verdognolo o in parte rossiccio." It would appear therefore that forms with dark red bines were not observed by him.

(3) Relative Number of Glands on the Leaves.

The under surface of the leaves bears yellow glands easily visible with a lens. It was found that the glands were more densely crowded on some plants than on others. In order to ascertain whether this character was of systematic value an estimate of the relative number of glands present on the leaves was necessary. For comparative results it was considered sufficient to record the number of glands found on a certain portion of each leaf examined, the area and situation of that portion being the same for all leaves. Countings were therefore made of the number of glands within a $\frac{1}{4}$ inch circle on that part of the leaf midway between the base of the lamina and one of the two sinuses at the base of the terminal lobe of the leaf; two countings were thus possible on each leaf, one on each side of the midrib¹. The countings were taken during from two to five seasons, several leaves being taken for each plant each year. The leaves were taken about half-way between the lower wire and the top wire, the examination being made as the plants came into flower.

Although there was considerable fluctuation in the number of glands occurring on leaves of the same plant taken in successive years and even on leaves taken from the same bine, nevertheless evidence was soon obtained that the leaves of some plants were more glandular than those of others. In 1916 and 1917 four or eight countings were made each year, according to the number of suitable leaves present on the plant at the time the examination was made; in subsequent years (1918-20) the greater number of plants which came under observation did not allow of so many actual countings but a sufficient number of leaves was examined to enable a general average or range of fluctuation to be estimated.

It was found that in some plants the number was invariably below the average, in others invariably much higher, while there were many transitional forms between the extremes. Examples are given in the following table, the figures, as explained above, showing the number of glands in a $\frac{1}{4}$ inch circle.

It will be observed that, of the three plants to which references have been made previously as being "very early" and having "green" bines, two, viz. Z 17 and Z 42, are included among those plants in which the leaf glands may be described as "many"; actual countings in the case

¹ For rapidity and convenience a thin piece of sheet metal, perforated at the centre with a circular hole $\frac{1}{4}$ inch in diameter, was placed on the leaf in the place indicated, and by means of a lens all the glands seen within the circle were counted.

of the third plant, OG 4, have not been taken but it has been noted that the number of glands on its leaves are above the average and in 1920 as many as 40 were counted to the $\frac{1}{4}$ inch circle. There seems to be no doubt therefore that OG 4 should be included with Z 17 and Z 42 among those plants with "many" leaf glands.

Glands few, moderate or many in number	Reference number of seedling	Male or Female	1916 (actual countings)	1917 (actual countings)	1918	1919	1920
Many ...	OB 17	♂	43; 47; 50; 43 58; 46; 27; 37	57; 45; 43; 56 51; 49; 49; 55	about 40	20—45	35—60
„ ...	OD 27	♂	—	59; 57; 49; 43 37; 42; 37; 44	about 40	22—31	27—39
„ ...	Z 22	♀	25; 26; 29; 30	43; 42; 35; 41 22; 26; 36; 35	about 25	30—50	about 35
„ ...	Z 17	♂	—	36; 30; 36; 29 28; 39; 24; 27	about 30	about 30	about 30
„ ...	Z 42	♂	—	55; 59; 64; 62 44; 39; 22; 47	about 40	about 30	about 30
Moderate ...	OA 39	♂	16; 20; 29; 31 13; 17; 15; 17	19; 20; 26; 18 11; 10; 20; 16	about 20	16—25	—
„ ...	Z 14	♂	12; 18; 26; 21 16; 13; 14; 16	17; 11; 10; 15 18; 11; 20; 21	about 20	about 20	19—35
„ ...	OA 59	♀	16; 25; 18; 13	18; 14; 23; 14 23; 17; 16; 20	about 15	15—20	15—21
Few ..	Z 43	♀	2; 3; 2; 7	3; 4; 4; 7	about 5	3—6	7—9
„ ...	OA 6	♀	4; 6; 2; 9	6; 9; 5; 10	about 5	3—4	6—9
„ ...	Z 58	♀	—	4; 2; 4; 4	about 5	1—5	2—6
„ ...	Z 49	♂	7; 6; 9; 10 10; 12; 9; 14	9; 11; 9; 12 9; 7; 7; 6	about 7	6—8	3—8
„ ...	Z 27	♂	6; 8; 12; 9 2; 7; 4; 5	8; 6; 9; 4 5; 7; 6; 5	about 8	3—10	4—15
„ ...	OA 28	♂	7; 4; 8; 12 9; 13; 4; 2	2; 3; 4; 5 5; 4; 3; 2	about 4	3—5	3—6

As in the case of the terms used to denote the "time of flowering" the terms "many," "moderate" and "few" used in the above sense are applicable only to the seedlings of the wild hop; the cultivated varieties of hop and their seedlings are generally far more glandular than these wild hop seedlings, plants with leaves having glands averaging over 60 in number to the $\frac{1}{4}$ inch circle being not infrequent in the former.

(4) *The Shape of the Leaves.*

The leaves of the mature plant are usually 3- or 5-lobed: those towards the apex of the stem being trilobed or entire. Occasionally however plants are met with which have a tendency to produce leaves with 7 or 9 lobes by the sub-division of the terminal lobe into three lobes, together with the division, in the 9-lobed leaves, of each basal lobe into two. The most striking case is that of a ♀ plant (Ref. No. 275)

which has only been under critical examination for two years but in both these years leaves with 7 lobes and others with 9 lobes were present.

This tendency was shown by two plants when grown under greenhouse conditions; these were the two "very early" ♂ plants Z 17 and Z 42. Cuttings from these two plants had been planted in pots and placed in the greenhouse to test their power of resistance to mildew under those conditions. Hop plants when grown in the small (about 5 in. diameter) pots used for these greenhouse trials generally give rise to small unlobed or 3-lobed leaves. In March 1920 four pots of Z 17 and five of Z 42 were producing young bines which at that time were about six inches high and the following notes were taken:

Z 17. In three pots the bines had 9-lobed leaves, i.e., of the five primary lobes the terminal was again 3-lobed and the basal lobes each 2-lobed. In the fourth was one bine only; this bore 9-lobed leaves below then 7- and 5-lobed forms and 3-lobed leaves above.

Z 42. In two pots the lower leaves were 5-lobed and the upper, 3-lobed; in another the leaves were 7-lobed (i.e. terminal lobe 3-lobed); in the fourth the leaves were all 5-lobed, while in the fifth the lower leaves were almost entire and the rest 3-lobed.

The tendency to produce leaves more divided than usual was thus very distinctly shown by Z 17, less distinctly by Z 42, and this was borne out by observations in the open, the original plants being carefully examined in the summer of 1920 when it was found that the leaves of Z 17 were 5—9 lobed while on Z 42 a few leaves with 7 lobes could be found and none with 9 lobes¹.

These 7- and 9-lobed leaves bear a close resemblance to those of a hop cultivated in Oregon known as the Oregon Cluster which appears to belong to the species *Humulus Americanus* Nuttall (see (1)).

One plant, OD 24, shows variation in the other direction, the leaves being 3-lobed only; the leaves of this plant have other characteristic features—they are dark green with a rather glossy surface and the lobes are narrower and more acutely pointed than in the usual type.

(5) Colour of the Leaves.

The range of colour shown by the leaves is not great but certain seedlings could be distinguished by having leaves evidently paler or darker than the majority. This character was not taken into account

¹ In Braungart's (3) work (p. 149), we find the statement: "In Weihenstephan war am Zaune des Hopfenvarietätengarten ein Wildhopfen, der öfter in der unteren Region 7 lappige Blätter hatte."

until 1919 when three plants, viz. J 11 (♀), W 49 (♂), OB 4 (♂), were observed with leaves which, compared with those of the plants around could be described as "light green"; all three in 1920 again had light green leaves. It would appear therefore that the pale colour is characteristic of these plants and is to be looked upon as a distinct variation from the normal type¹. The three very early ♂ plants, Z 17, Z 42 and OG 4 have also a tendency to produce leaves of a paler green than is usually met with. Several plants had been noted in 1919 as having "rather light green" leaves and the same description was applicable in 1920 to some of them; others however showed no distinctive paler colour in 1920 and in these cases the change was probably merely of the nature of seasonal fluctuation.

BB 16 (♀) is a plant which had leaves of a "dark green" colour as compared with surrounding plants, in 1919, and the same character re-appeared in 1920. OD 24 (♀) is another plant with dark green leaves.

(6) *The Length of the Laterals.*

In the great majority of cases the laterals (primary branches of the main stems) reach a length of from four to five feet. In some instances however plants which have consistently produced laterals of a much shorter length have been noted. An extreme case is OA 5 (♂) a plant which has been under observation for five seasons but has never produced laterals exceeding one foot in length; this plant has also short bines which usually do not reach the top wire (see above, p. 243), while the plants with long laterals have bines which readily reach the top wire and grow along it or fall over to produce a dense "head" of leaves and inflorescences. Other plants with laterals shorter than the average are

W 36 (♂), maximum length of laterals about 2 ft. 6 inches,

Z 58 (♀), OD 24 (♀), OC 11 (♂) maximum length of laterals about 3 ft.

Plants of this type, when compared with the usual type, show a lack of vigour, the bines being shorter and thinner. Whether this is due to a pathological condition or whether the plants possess a factor for "shortness" is not known. This shortness of bines and laterals would seem however to be an inherent character of some hop plants. Thus in the hop-garden at Wye College there is a ♂ hop plant Ref. no. J 36 (seedling of a cultivated variety) which was planted out in 1911 and has

¹ Varieties (♂ and ♀) of *H. Lupulus* possessing "golden" (yellow-green) leaves are known(7).

been observed through nine seasons; during this period the laterals have never exceeded a length of fifteen inches and the plant shows no evidence of ill-health.

(7) *Characters associated with the Reproductive Organs in the ♂ plants.*

In the ♂ plants, as seen by the naked eye, no variation has been observed in the general appearance of the flowers. When examined with a lens however glands are to be observed on the perianth-lobes, on the anthers (along the furrow)¹ and, in some plants, on the receptacle. There is evidence of variation in the glandulation of these organs.

Glandulation of the perianth lobes. The number of glands on the perianth lobes varies with the insertion of the lobes on the short axis bearing them. Of the five lobes forming the perianth of a flower, the two lower ones (the outer ones of the bud) almost invariably bear very few or no glands; the inner lobes are generally far more glandular than the outer ones and the innermost lobe may bear glands to the number of twenty or even more. As a criterion of the variation in the glandulation of the perianth lobes therefore only the innermost one is taken into consideration and the numbers given below have that reference.

The number of glands on the innermost perianth lobe is generally from 10 to 15. In some plants the number was found, during five years, not to exceed 10; in others the number has generally been about 20, while in one instance 30 glands were found on a single lobe. When the number is consistently below 10 the plant may be described as having "few perianth glands"; when the number is usually twenty or more the plant is classified as having "many perianth glands."

The following Table shows the maximum number of glands found on the perianth lobes of certain plants during five years (three years in one case).

Maximum number of glands recorded for innermost perianth lobe.

	Reference number of seedling	1916	1917	1918	1919	1920
Plants with "many" perianth glands	OA 61	20	28	18	21	22
" " "	OE 23	—	—	30	26	24
Plants with "few" perianth glands	Z 27	9	8	6	8	10
" " "	OA 2	5	4	12	9	8
" " "	OA 4	4	6	8	7	8
" " "	OA 28	2	6	8	9	6
" " "	OC 6	8	7	6	8	7

¹ Glands on the perianth lobes and anthers of the ♂ hop plant have been recorded by Parlature (*Flora Italiana*, Vol. iv. p. 304) and figured by Braungart (3) (p. 206).

The Glands of the Stamens. The glands of the stamens are situated in the furrow on the dorsal surface of the anthers. They usually form a single row along the furrow but when numerous some are out of line with the rest. The number usually varies from 1 to 6. A few extreme types that have been met with are suggestive that some plants have a tendency to produce more, others less, glands than the average. At the two extremes are HH 11 and BB 35 of which the figures recorded as showing their fluctuation during three successive years are as follows, the first figure in each case being the lowest number observed, the second the highest :

	Reference number of plant	1918	1919	1920
Plant with "many" anther glands	HH 11	8—13	6—11	4—10
" " "few" "	BB 35	0 or 1 (rarely 2)	0—2	0—2

Others in which the difference is less pronounced, observations having been made for 3, 4, or 5 years, are :

	Reference number of plant	1916	1917	1918	1919	1920
Plants with a tendency to produce many anther glands	OA 15	3—12	2—10	6—11	2—8	3— 8
	OA 43	4—10	4— 8	6—11	3—7	—
	OD 27	—	4—10	5—14	3—8	5— 8
	Z 15	—	6—10	5—13	4—8	3—10
	Z 51	3— 7	3— 9	2— 7	4—7	4— 9
Plants with a tendency to produce few anther glands	OB 14	1— 6	0— 3	0— 3	0—3	—
	OD 7	0— 3	1— 4	1— 3	1—2	—
	Z 31	0— 4	0— 4	0— 3	0—6	0— 4
	Z 33	1— 4	1— 5	0— 3	0—5	—
	1/55	—	—	0— 3	0—2	0— 3

Glands on the receptacle. During an examination (see (2)) of male hop plants grown from seeds collected from cultivated varieties of hops it was noticed that in most cases glands were present on the inner surface of the receptacle round the insertion of the stamens. In the seedlings from the wild hop however glands are usually absent from the receptacle which is frequently more or less tumid forming a "disc"; thus in nearly every case the receptacle glands were recorded as 0 or 0(1), rarely 0(1—2), indicating that occasionally one gland, rarely two, could be found and it was not always certain that in these cases the glands had not fallen into the receptacle from the anthers. The only plant which has shown any consistent deviation from the usual type with respect to the receptacle glands is HH 35 of which the records for the three years during which it has been examined are 0—4, 4—10 usually (but occasionally 0—3), 2—9¹.

¹ A plant which has shown extraordinary fluctuation from year to year in the number of glands present on the receptacle is OA 47. In 1916 and 1917 the flowers of this plant had comparatively a large number of glands on the receptacle. During these two years

Characters associated with the Reproductive Organs in the ♀ plants.

No differences, apart from the time of flowering, were detected in the pistillate spikes of the female plants but as the "hops" reached maturity variation was observed with respect to (1) size and shape of the hops, (2) "condition" (richness in lupulin glands), (3) aroma, (4) colour of "strig" (axis of the strobile).

Size and Shape of the Hops. As already pointed out these seedlings of the wild hop plant are on the whole much later in flowering than the commercial varieties grown in this country; in consequence the hops of many of the plants never grow out to their full size; their lateness, again, makes those plants which are susceptible to mildew liable to infection when in the "burr" or flowering stage so that in many cases the plant has to be recorded year after year as "crop destroyed by mildew." Thus the characters of the hops of some plants could not be taken at all and those of other plants could only be recorded in one or two seasons. A good proportion however yielded hops which were available for examination in from three to five seasons and the evidence obtained indicates that some plants have a tendency to produce, in successive years, hops larger than the average and a few produce relatively very broad hops.

As the hops even on one bine vary considerably in size it was decided to take for measurement only the largest well-developed ones. It was found that in the majority of the plants the well-developed hops varied in size from 1.0×0.6 inches to 1.3×0.8 inches and were generally ovoid to ovoid cylindrical in shape. The Table below shows the fluctuation

Length of well-developed hops in inches.

	Reference number of seedling	1916	1917	1918	1919	1920	Date of flowering in 1919
Plants with small hops	Z 20	1.0	1.2	1.1	1.2	0.9	Aug. 22
	Z 22	—	1.2	1.1	1.1	1.2	Aug. 31
	Z 25	1.1	1.2	1.2	1.2	1.1	Aug. 19
Plants with hops of a larger type	FF 7	—	—	1.4	1.7	1.2	Aug. 30
	OC 39	—	1.6	1.5	1.6	—	Aug. 30
	OD 17	1.3	—	1.5	1.4	1.4	Aug. 20
	BB 31	—	—	1.4	1.7	1.3	Aug. 27

the vigour of the plant was apparently normal, except that in 1917 the laterals were shorter than in the previous year; notes show that the plant in 1918 was "rather weak," in 1919 it was "weak, with small leaves," while in 1920 it reached only to about half its usual height and bore no flowers. The glands on the other organs however did not show a corresponding diminution in number, in fact those on the leaves showed an increase after the first year. The glands on the receptacle of this plant were recorded as follows:

1916	1917	1918	1919	1920
2—12	1—8	0—4	0 (1)	no flowers present.

in the length of the hops of certain plants which have consistently produced hops larger than the average and of others which have always developed small hops. The date on which the plants came into flower (stigmas showing) in 1919 is also given to show that the plants with small hops were, on the average, not later than those which produced the larger hops.

With regard to the shape of the hops three plants have been noted as producing hops relatively broader than the average; the well-developed hops on these are about $\frac{1}{5}$ inch broader than hops of the same length on other plants, and may be described as broadly ovoid. This difference is sufficient to make the individual hops appear almost spherical and when the crops are seen in mass the plants have a characteristic appearance.

The fluctuation in the size of the hops from year to year in the same plant shows in most cases such a wide range compared with the differences found between individual plants that the value of "size of hops" as a systematic character is doubtful and will require further observations to determine the stability or otherwise of this character in the type plants quoted in the table.

On the other hand the "broadly ovoid" type of hop appears to be a distinct variation from the ordinary type. Of the three plants mentioned as showing this character the dimensions of the hops were taken only during 1919 and 1920 though the hops of all three had been previously denoted as "broadly ovoid." The recorded dimensions of the hops of these three plants are

Reference number of seedling	1919	1920
OA 59	1.5×1.1	1.2×0.9
Z 22	1.1×0.9	1.2×0.9
OK 55	1.3×1.0	1.2×0.9

"Condition." The resins to which hops owe their preservative and bittering properties are secreted within the lupulin glands which develop chiefly at the basal portion of the bracteoles of the cones. If a ripe hop is torn or cut longitudinally or transversely the glands are seen as a golden yellow powder around the axis of the cone. According to the relative number of glands present as indicated to the naked eye by the intensity of the golden yellow colour the "condition" was recorded as poor, fair, good or very good. In most of the plants the "condition" fluctuated from year to year between fair and good. A few plants however were con-

sistently good to very good during the years they were under examination while others were only recorded as poor or fair¹.

Generally speaking it was found that those plants which have good condition have more glands on the leaves than those which have poor or fair condition; this is shown in the following table:

Reference number of seedling	1916	1917		1918		1919		1920	
	Leaf glands	Leaf glands	Condition	Leaf glands	Condition	Leaf glands	Condition	Leaf glands	Condition
OA 34	11—20	—	v. good	—	v. good	about 50	good	21—38	good
OA 29	15—27	25—47	v. good	about 25	v. good	about 30	good	about 30	good
Z 30	20—35	19—32	v. good	about 35	v. good	25—30	v. good	28—37	good
88	—	—	—	—	v. good	about 20	good	27—39	good
OD 19	6—18	—	—	about 15	fair	5—9	fair	about 6	fair
OK 55	—	—	—	about 15	—	about 10	poor to fair	—	fair
BB 5	—	—	—	about 5	—	1—3	fair	1—2	poor
Z 43	2—7	3—7	fair	about 5	—	3—6	fair	7—9	fair
OA 59	13—25	14—23	poor	about 15	—	15—20	fair	15—21	fair

By *Aroma* is here meant the smell given off by the fresh ripe hop when bruised or broken; it is due to the essential oils contained in the lupulin glands. In many cases the hops never became ripe enough to give a distinctive aroma, while in others the aroma was not strong enough to be distinctive even in the ripe hops. A few seedlings however gave year after year an aroma comparable with that of good commercial varieties, while in other seedlings the aroma was very strong and unpleasant, almost nauseating².

The records of a few of the typical plants are given for comparison.

Reference number of seedling	1917	1918	1919	1920
OD 19	very pleasant	pleasant	pleasant	very pleasant
OA 34	pleasant	very pleasant	pleasant	pleasant
OB 9	pleasant	pleasant	pleasant	pleasant
88	—	pleasant	pleasant	pleasant
BB 16	—	very unpleasant	very unpleasant	very unpleasant
OD 20	—	strong, unpleasant	very unpleasant	very unpleasant
OF 19	—	very unpleasant	very unpleasant	very unpleasant
FF 35	—	very unpleasant	very unpleasant	unpleasant
AA 5	—	unpleasant	very unpleasant	very unpleasant

In the above plants there was no doubt as to the "pleasantness" or "unpleasantness" of the aroma; in others however the aroma was less distinctive and it was often difficult to decide into which category a particular aroma should be placed, especially as in some cases the scent would at first seem pleasant but this after a few seconds was replaced by one which could only be called unpleasant.

¹ Braungart (3), p. 209, observes that the "condition" ("Sekretgehalt") varies with different plants of the wild hop.

² No pronounced garlic-like smell was met with in the green hop.

There appears to be no correlation of "condition" and aroma; thus

88 and OA 34	have condition good to very good, aroma pleasant to very pleasant			
OD 19	has	„	fair	, „ pleasant to very pleasant
AA 5	„	„	good	, „ unpleasant to very unpleasant
OF 19	„	„	fair	, „ very unpleasant

Colour of the Strig. A range of colour similar to that of the bines also obtains in the strigs of the hop cones. "Strig" is the name commonly used to denote the axis of the hop cone; on the swollen nodes of this axis are inserted the flowers with their accompanying bracts and bracteoles. The nodes of the strig are usually of a darker colour than the internodes. In most of these plants the internodes are reddish with the nodes a dark purplish red. In extreme cases the strig is pale green with usually a faint reddish tinge at the nodes, or the strig is dark red throughout. The colour in individual plants fluctuates to some extent even in the hops of the same year; certain plants however produce green strigs (green throughout or green with reddish nodes) year after year while others consistently produce red strigs (red internodes and dark red nodes or strig red throughout).

It was expected that the colour of the strig would be correlated with that of the stem. Of those plants with red bines most had red strigs with dark red nodes, a few had strigs dark red throughout while in some the strigs were green with pale reddish nodes. Only one of the ♀ plants had green bines; unfortunately this plant became diseased and had to be destroyed before the hops matured and so the colour of the strig was not determined. Those plants of which the bines were intermediate in colour between the green and the red plants had strigs which were almost invariably recorded as green (or faintly reddish) with reddish nodes. It would appear therefore that there is a tendency for the plants with red bines to produce red strigs and those in which the red colour of the bines is less pronounced to produce green or pale reddish strigs. As is well known the green-bined cultivated varieties of hop have green strigs.

One plant, Z 58, has strigs which have a polished (vermicose) appearance; this character has appeared, though not so pronounced, in two other plants.

(8) *Degree of susceptibility to the mildew Sphaerotheca Humuli (DC.) Burr.*

Accounts have already been published ((4) to (7)) of the differences shown by individual seedlings as regards susceptibility to the attacks of the Hop Mildew. A résumé of the chief facts observed will be given, and

then the question considered as to whether any correlation with morphological characters exists—a point not hitherto dealt with.

The method of testing the individual seedlings for susceptibility to mildew was as follows. The seedlings when 1- or 2-years old, were exposed to infection in the greenhouse by being constantly inoculated with *conidia* under conditions very favourable to the growth and spread of the mildew. During the following winter these seedlings were planted out in the Experimental Hop-garden, where natural inoculation by the mildew was relied upon—a method found to be quite satisfactory. Owing to the late-flowering habit of the seedlings it was found that October was the best month for examination as to the incidence of mildew in the open. In the case of the ♀ plant, the production at the end of August and during September of the female inflorescence and young developing hops provided the best possible infectible material. With the ♂ plant, the infectible material in the autumn consisted for the most part of the young leaves of the axillary side shoots which developed from the lower portion of the main stem. Mildew was prevalent generally in the Hop-garden in the autumn of each season from 1916 to 1920, and particularly severe outbreaks occurred in 1916, 1919 and 1920. From 1914 onwards 480 seedlings were kept under observation; first as seedlings in the greenhouse and then in the Hop-garden where they grew on to mature plants.

From the *data* contained in the Table on p. 259, it will be seen that different seedlings—exposed in the open to identical conditions of soil and weather¹—showed very different reactions to the attacks of the mildew.

In the case of the most susceptible ♀ plants (indicated by the sign *S*³ in the above Table) the greater proportion of the “hops” (cones) were deformed by the mildew year after year, or not infrequently the whole crop of “hops” was entirely destroyed, the female inflorescences being attacked when quite young and their further development permanently arrested, the inflorescences becoming converted into white “knob”-like growths (see Pl. XXV, fig. 1). With the most susceptible ♂ plants, the mildew sometimes invaded the branches of the inflorescence.

On the other hand, complete or almost complete resistance to mildew was shown in the open by certain individual seedlings, both ♂ and ♀.

Where, in the Hop-garden, such resistant seedlings grew side by side with the very susceptible plants, the contrast, season after season, was

¹ The seedlings being all “trained” the same way ensured similarity of conditions as regards illumination.

Table showing the degree of susceptibility to mildew in the greenhouse (G),
and in the Hop-garden (H).

Reference number of seedling	Sex	1916		1917		1918		1919		1920	
		H	G	H	G	H	G	H	G	H	G
V 91	—	—	O	—	O	S ¹	—	O	O	O	O
V 92	—	—	O	—	O	S ¹	—	O	O	O	O
V 93	—	—	O	—	O	S ¹	—	S ¹	O	O	O
Z 1	—	—	—	S ²	—	S ²	—	S ²	—	S ¹	—
Z 2	—	—	—	O	O	O	O	O	O	O	O
Z 14	—	—	—	O	—	S ¹	O	O	O	S ¹	O
Z 15	—	—	—	S ²	—	S ²	$\frac{1}{2}S$	S ²	$\frac{1}{2}S$	$\frac{1}{2}S$	$\frac{1}{2}S$
Z 22	—	—	—	O	—	S ¹	O	S ²	O	S ¹ or S ²	O
Z 23	—	—	—	S ²	—	O	$\frac{1}{2}S$	S ¹	$\frac{1}{2}S$	—	$\frac{1}{2}S$
Z 24	S ³	—	—	S ³	—	S ³ †	—	S ¹	S	S ² †	S*
Z 25	O	—	—	O	—	O	O	O*	O	S ¹	O
Z 26	S ³	—	—	S ¹	—	S ³	—	S ²	S	S ² †	S*
Z 38	—	—	—	S ²	—	S ²	—	O	—	—	$\frac{1}{2}S$
Z 39	—	—	—	S ³	S	S ³ †	S	S ²	S*	—	S
Z 41	—	—	—	S ³	—	S ²	—	S ³	—	S ³ †	S*
Z 42	—	—	—	O	—	O	O	—	O	—	O
Z 43	—	—	—	S ²	—	S ²	—	S ¹	—	S ²	—
OA 25	—	—	—	S ²	—	S ³	—	S ¹	—	S ¹	S
OA 26	—	—	—	S ³	—	S ³ †	—	S ³ †	S*	S ³ †	S*
OA 33	—	—	—	O	—	O	$\frac{1}{2}S$	S ²	$\frac{1}{2}S$	S ¹	$\frac{1}{2}S$
OA 34	—	—	—	S ²	—	S ²	—	S ¹	O	S ¹	O
OA 35	—	—	—	S ³	—	S ³ †	—	S ³ †	S	S ² †	S
OA 49	—	—	—	O	—	O	O	O	O	S ¹	O
OB 34	—	—	—	O	—	S ¹	O	—	O	O	O
OC 6	—	—	—	O	—	O	$\frac{1}{2}S$	S ¹	$\frac{1}{2}S$	$\frac{1}{2}S$	$\frac{1}{2}S$
OD 16	—	—	—	S ³	—	S ³ †	—	S ²	S	S ² †	S
OD 17	—	—	—	S ¹	—	S ¹	—	S ¹	$\frac{1}{2}S$	S ¹	$\frac{1}{2}S$
OD 18	—	—	—	S ³	—	S ³ †	—	S ³	—	S ³ †	S*
OD 19	—	—	—	O	—	O	O	S ¹	O	S ¹	O
OR 38 ¹	S ¹	—	—	S ²	O	S ³	O	S ¹	O	S ²	O
OR 39 ¹	S ¹	—	—	S ¹	O	O	O	O	O	O	O

S¹=mere trace of mildew; S²=fair amount of mildew; S³=plant very mildewed. S³† indicates that the crop of hops was destroyed by mildew. S indicates that the plant under greenhouse conditions was normally susceptible to mildew, and S* that extreme susceptibility was shown. O=no mildew present. — indicates that no record was available.

Where running numbers occur, e.g., V91, V92, &c., the respective seedlings were growing next to each other in the same row and 3 ft. 6 in. apart.

** A few small patches of mildew appeared on August 7, on a few of the young leaves, after a spell of abnormally cold, dull weather. The mildew patches soon died away and in October the plant was entirely free from mildew.

¹ OR 38 and OR 39 were both immune in the greenhouse in 1914.

most marked. Thus the ♀ seedling OD 19 remained entirely free from mildew through the seasons 1917 and 1918 and showed only the merest trace of mildew in 1919 and 1920, while the ♀ seedling OD 18 planted next to it and growing so close that the lateral branches of each became intertwined, was so susceptible to mildew that each year the hops and the leaves were infected to the degree of S³ and in 1918 and 1920 the crop of hops was completely destroyed by mildew. A photograph taken

in 1920 is given in Pl. XXV, fig. 2 showing a "lateral" of OD 18 twining round a lateral of OD 19; OD 18 is so virulently infected with mildew that no "hops" have been able to develop, all the inflorescences having been turned into little white "knobs," while the hops of OD 19 have resisted all attacks and developed normally, quite free from a trace of mildew.

Complete immunity to mildew was shown by 27 seedlings (13 ♂, 14 ♀) when grown in the greenhouse. When cuttings were taken from these seedlings after they had been growing for several years (in one case 5 years) in the (manured) hop garden, they showed the same complete immunity in the greenhouse. On the other hand, cuttings taken from other seedlings which showed varying degrees of susceptibility in the Hop-garden were susceptible when grown in the greenhouse. In no case has any seedling which has shown immunity in the greenhouse shown susceptibility there when tested again in other seasons.

Seedlings immune in the greenhouse show usually some degree of susceptibility when tested in the open, the degree of susceptibility being usually only very slight, but in rare cases reaching to S^2 or even to S^3 . (See Table, p. 259.)

Certain individual seedlings (7 in number, 4 ♂ and 3 ♀) showed the phenomenon ((6) (7)) of "semi-immunity" when grown in the greenhouse; these seedlings exhibited in the open also a certain degree of resistance.

A numerical analysis of the 480 seedlings based on the relative susceptibility to mildew in the open gives us the following figures:

Degree of susceptibility	Number of seedlings	Percentage
S^3 (including $S^3 \uparrow$) each year { (11 ♂; 85 ♀) }	96	20.00
S^2 to S^3 (sometimes $S^3 \uparrow$) { (35 ♂; 80 ♀) }	115	23.96
S^2 { (54 ♂; 26 ♀) }	80	16.67
S^1 to S^2 { (41 ♂; 48 ♀) }	89	18.54
S^1 { (19 ♂; 12 ♀) }	31	6.46
$O-S^1$ { (9 ♂; 9 ♀) }	18	3.75
O { (all ♂) }	6	1.25
$O-S^2$ { (9 ♂; 18 ♀) }	27	5.63
$O-S^3$ { (all ♀) }	3	.60
S^1 to S^3 { (5 ♂; 10 ♀) }	15	3.12
Totals	480	100

Of the 480 seedlings raised, 189 plants (39·38 %) proved to be ♂, and 291 (60·62 %) ♀.

A separate analysis of the records of the two sexes gives us the following figures :

Analysis of 189 ♂ seedlings of the "wild hop."

Degree of susceptibility	Number of seedlings	Percentage
S^3	11	5·82
$S^2—S^3$	35	18·52
S^2	54 ¹	28·57
$S^1—S^2$	41	21·69
S^1	19 ²	10·05
$O—S^1$	9 ³	4·76
$O...$	6 ⁴	3·17
$O—S^2$	9 ⁵	4·76
$S^1—S^3$	5	2·65
Totals	189	100

Analysis of 291 ♀ seedlings of the "wild hop."

Degree of susceptibility	Number of seedlings	Percentage
S^3 (including S^3+) ...	85	29·21
$S^2—S^3$ (sometimes S^3+)	80	27·49
S^2	26	8·93
$S^1—S^2$	48	16·49
S^1	12	4·12
$O—S^1$	9	3·09
$O—S^2$	18	6·19
$O—S^3$	3	1·03
$S^1—S^3$	10	3·44
Totals	291	100

The percentage figures in the two tables given above indicate a higher degree of susceptibility in the ♀ seedlings than in the ♂. It would be unsafe, however, to consider this proved, owing to the circumstance that the observations as to the incidence of the mildew were made at a time peculiarly favourable for attacks on the ♀ plant. The ♂ and the ♀ plants would need to be tested at a time when each provided the same amount of infectible material before any inference could safely be drawn as to their relative susceptibility.

Since excellent material to test the susceptibility was always present in the case of the ♀ plant, it appears safe to use the analysis of the records of the 291 ♀ seedlings on which to base an estimate of the

¹ Of these, 1 seedling was semi-immune in the greenhouse.

² Of these, 3 seedlings were immune in the greenhouse.

³ Of these, 5 seedlings were immune, and 1 semi-immune, in the greenhouse.

⁴ Of these, 5 seedlings were immune in the greenhouse.

⁵ Of these, 2 seedlings were semi-immune in the greenhouse.

percentage of seedlings occurring in the different grades of susceptibility.

In the highest grade of susceptibility, in which the plant was *each season* mildewed to the extent of S^3 , there are 85 seedlings. Our records show that of these 85 seedlings, no less than 34 had the crop of "hops" entirely destroyed by mildew in one or more seasons¹.

In the next class, the incidence of mildew varied from S^2 to S^3 in different seasons. This class comprises 80 seedlings; of these, 21 seedlings were attacked in some season to the extent that the entire crop was destroyed².

If we add together the numbers 34 and 21, we get 55 as the number of seedlings which have had their entire crop of hops destroyed in some season or seasons. This number represents 18.90 % of the total number of the ♀ seedlings.

We may consider the class of 85 seedlings attacked S^3 each season—representing 29.21 % of the ♀ seedlings—as exhibiting excessive susceptibility to mildew, probably exceeding that shown by any commercial variety of hop cultivated to-day.

To the class of very susceptible seedlings may safely be added the 80 seedlings of the S^2 — S^3 class. This gives us 165 seedlings (or 56.70 % of the total number) belonging to a grade of susceptibility in which virulent attacks of mildew are common.

In the class S^2 , consisting of seedlings which have shown a medium attack of mildew each season, we have 26 plants, or 8.93 %.

In the next class, where the incidence of mildew varies in different seasons from S^1 — S^2 —that is, from a trace of mildew to a medium attack—we have 48 seedlings, or 16.49 %. In this class an appreciable degree of resistance to the mildew begins to be shown by some of the seedlings, but it is in the succeeding classes that this phenomenon is most clearly seen.

In the class S^1 , i.e. those seedlings which have shown only a trace of mildew each season, we have 12 plants. Of these, 5 cannot be considered to have been sufficiently tested, leaving us with 7 seedlings which have proved to be persistently resistant in the open. Of these 7 seedlings, 4 are immune and 1 semi-immune, under greenhouse conditions.

¹ The actual records for these 34 seedlings are as follows, where the integer gives the number of seedlings, the numerator of the fraction the number of times the entire crop was destroyed and the denominator the total number of seasons during which observations were taken: 2, $\frac{3}{4}$; 5, $\frac{2}{4}$; 7, $\frac{1}{4}$; 2, $\frac{2}{3}$; 7, $\frac{1}{3}$; 11, $\frac{1}{2}$.

² In all cases S^3 † was reached only once by these seedlings, the actual records being as follows: 1, $\frac{1}{5}$; 9, $\frac{1}{4}$; 6, $\frac{1}{3}$; 5, $\frac{1}{2}$.

In the class $O-S^1$ we have 9 seedlings, of which 1 has been insufficiently tested. Of the remaining 8, 6 are immune, and 1 semi-immune, under greenhouse conditions.

In the class $O-S^2$, in which there are 18 seedlings, 2 plants (both of which show immunity in the greenhouse) have proved decidedly resistant in the open, the grade of infection only very rarely reaching to S^2 . The other seedlings in this class, while certainly showing some resistance to the mildew, are liable to fairly serious attacks in some seasons. Among these seedlings are 2 which are immune, and 1 which is semi-immune, under greenhouse conditions.

The 13 seedlings in the classes $O-S^3$ and S^1-S^3 do not constitute in either case a proper group. Of the 3 seedlings showing $O-S^3$, one only probably possesses a slight degree of resistance. Of the 10 seedlings showing S^1-S^3 in different seasons, 9 almost certainly belong to the S^2 or S^3 class, while the remaining seedling, OR 38, which is immune in the greenhouse, is exceptional in showing in the open as high a grade of susceptibility as S^2 in some seasons.

The degree of susceptibility to mildew shown by the seedlings has no correlation, so far as we can see, with other characters. Thus among the resistant plants are some with green bines others with red bines, some are early, others late, some have many glands, others few, and similarly with the very susceptible plants. Again, plants which are indistinguishable in other ways show different powers of resistance towards the fungus as shown by the following records:

Description of plants	Reference number of plant	1917		1918		1919		1920	
		H	G	H	G	H	G	H	G
♂ very early, green bines, many leaf glands, few perianth glands, rather pale leaves	Z 17	O	—	—	—	—	O	—	O
	Z 42	O	—	O	O	—	O	—	O
	OG 4	—	—	S^2	—	S^2	—	S^3	—
♀ late, red bines, few leaf glands, condition fair, aroma pleasant, strig red	OA 49	O	—	O	O	O	O	S^1	O
	OB 6	S^3	—	S^3	—	S^3	—	S^3+	—
♀ midseason, red bines, few leaf glands, condition poor to fair, strig red (aroma generally more pleasant in OD 19 than in OD 16)	OD 19	O	—	O	O	S^1	O	S^1	O
	OD 16	S^3	—	S^3+	—	S^3	S	S^3+	S
♀ late, red and green (mottled) bines, many leaf glands, condition fair to good, aroma pleasant, strig reddish with darker nodes	Z 22	O	—	S^2	O	S^2	O	S^1 or S^2	O
	OG 28	—	—	S^3	—	S^3	—	S^3+	—

As regards the characters taken, then—which comprise the most important morphological ones—for many (if not all) of the “immune” forms there appear to be susceptible forms which are similar morphologically. It is to be noted that similar forms in other species of plants

have been met with, both in nature and also among the hybrid offspring produced in certain breeding experiments.

One of us has pointed out (8) that within the species *Bromus mollis* two "races" exist, morphologically identical but one susceptible, and the other immune, to certain forms of the mildew *Erysiphe Graminis* DC.

Vavilov (9) states that *Triticum dicoccum* comprises, with respect to *E. Graminis*, both susceptible and immune races¹.

Biffen (10), commenting on the characters of the hybrid plants raised by crossing "Michigan Bronze" (a wheat susceptible to the rust *Puccinia glumarum*) with "American Club" (immune), says: "The two parents differ from one another in other characters besides the immunity and liability to the attacks of rust, and it may be noted that, as one would expect, individuals similar to the immune parent morphologically but susceptible to rust were found, and also the rust-proof form of the susceptible parent²."

General Considerations.

The various characters reviewed above would appear to have varietal significance, for not only do they persist from year to year in the same individual but all the evidence to hand suggests that many—if not all—of the characters mentioned would reappear on propagating the plants vegetatively³. Thus two plants have been raised by "cuttings" from a ♀ seedling (OR 38) and one plant from a ♂ seedling (Z 11); it was found that the plants raised by cuttings were similar to the original plants in time of flowering, colour of bine, glandulation of leaves and ♂ flowers, "condition," aroma and colour of the "strig" of the hop-cone, and degree

¹ On the general question, Vavilov (9), p. 52, remarks: "the physiological individualisation of race is very often accompanied by morphological characters which, however, are externally not very conspicuous. In these cases the peculiarity in behaviour towards fungi obliges the observer to pay more attention to this or that previously unsuspected race, and in the end he usually succeeds in finding in it some other confirmatory differences."

² In another case, it was found that no correlation existed between the leaf-characters of the parent varieties of wheat used in "crossing" and susceptibility to rust—"the immunity [in the F_2 generation of the hybrids] simply depended on the luck of the shuffle" (Biffen (11)).

³ This has been shown ((2), p. 177), by systematic records to be the case with the corresponding characters of ♂ plants raised from seeds taken from cultivated varieties. It is also to be noted that the characteristic features of certain recognised commercial varieties (which are propagated vegetatively by cuttings) are of the same order as some of the characters discussed in this paper, e.g., early flowering ("Early Bird" variety), pale green bine ("Canterbury Whitebine"), very pleasant aroma ("Goldings"), large size of hop "cone" and strong aroma ("Fuggles").

of susceptibility to mildew. Again, a large number of "cuttings" have been taken from a large number of seedlings some of which were immune from, and the rest susceptible to, mildew in the greenhouse; the distinctive characters of each seedling remained constant¹.

A certain range of variation is found in each series of characters, the extreme forms in some series being widely different, as in the green-bine and the red-bine forms, and in the resistant and the very susceptible (to mildew) forms. There is no evidence of correlation of any one character with the others, with the possible exception of the case of the three very early ♂ plants in which very early flowering is associated with a green bine and many leaf-glands. The cases of apparent correlation (to which reference has been made on p. 256) between (1) the number of glands on the leaves and the "condition" of the hop-cone, and (2) between the colour of the bine and petiole and the colour of the strig, cannot perhaps be considered as the association of distinct characters but rather as manifestations of the one character (glandulation in the one case—production of a red colouring matter in the other) in different organs.

A classification to include all forms is at present impossible as the evidence at hand suggests that given an unlimited number of seedlings a gradual transition would be found between the extreme types of each series and even an approximate estimate of the possible number of combinations of characters cannot be given.

The accompanying table however may prove of interest as indicating the combinations of character with respect to time of flowering, colour of bine and the relative number of glands on the leaves as shown by the

		Colour of the Bines								
		Green			Mottled green and red			Red		
		Many	Moderate number	Few	Many	Moderate number	Few	Many	Moderate number	Few
Time of Flowering	Early (*very early)	3*	—	—	3	2	1	3	5	6
	Midseason	—	—	—	3	4	6	17	46	49
	„	1	—	—	4	2	3	22	62	42
	Late	—	—	—	1	—	—	4	3	1
	„	—	—	—	2	3	2	11	50	28
Relative number of Glands on the Leaves										

¹ No "cross"-breeding of the different forms has yet been carried out. Seeds collected from "open" flowers of a ♀ seedling (Z 25) immune to mildew produced 33 seedlings, which when tested for mildew-susceptibility in the greenhouse, proved to consist of 24 immune and 9 susceptible plants (7).

395 plants which have been examined; the figures indicate the number of plants in which any particular combination in the three series was found.

It is to be observed that the above divisions are altogether arbitrary and only show the range of variation in the plants which came under observation; with a large number of plants probably more extreme cases would be met with making necessary a modification of the divisions. It is also to be noted that only the extreme forms and the obviously intermediate ones can be readily assigned to their particular divisions; the rest are placed as they tend on the whole, with the records to hand, towards one or the other extreme or towards the intermediate type¹. Thus with the three series of characters selected, each considered as comprising three divisions, there are 27 possible combinations of characters for each sex, of these 17 have been observed among the ♂ plants and 16 among the ♀ plants in an examination of 395 plants in all.

It will be seen from the table that the great majority of the plants have red bines, that most of these again are included under "midseason" or "late," and have few (or a moderate number of) glands.

Of all the plants examined not one has proved to be of any commercial value, the majority being much too late and all having hops too small to make cultivation of the plants a profitable undertaking under modern conditions. The fact that resistance to Hop Mildew is a character of some of the seedlings suggests that this desirable quality might by breeding operations be combined with other qualities of a good hop; in one plant, OA 34, it is combined with relatively good "condition" and a pleasant aroma.

We have not been able to find any detailed account of variations observed in the wild hop. Braungart (3), in his elaborate monograph on the cultivated varieties of the hop, deals only very cursorily with the wild species². Systematists have separated one variety, viz. *brachystachyus* Zapal. *Consp. Fl. Galic.* II. 94 (1908), described as follows:

¹ No individual seedling has been met with which, as regards the characters noted in the present paper, has shown fluctuations ranging from one extreme to the other.

² Braungart (3), p. 146, referring to the wild hop growing in Switzerland, says: "Die in unmittelbarer Nähe stehenden Individuen sind sich dabei oft nach allen Richtungen, auch in den Zapfen, sehr ähnlich, oft aber auch nicht, und weiter entfernt voneinander stehende sind meist nach allen Beziehungen sehr abweichend." In a paper by J. Schmidt (*C. rend. trav. Lab. Carlsberg*, Vol. XI, 314—329 (1917)) entitled "The occurrence of the wild hop in Denmark," a reference is made to "the numerous forms in which this plant occurs" but their distribution, and not their characteristics, is mainly discussed. Further, Schmidt uses the term "wild" merely to indicate "not cultivated," and it seems probable that he is dealing partly with escapes from cultivation.

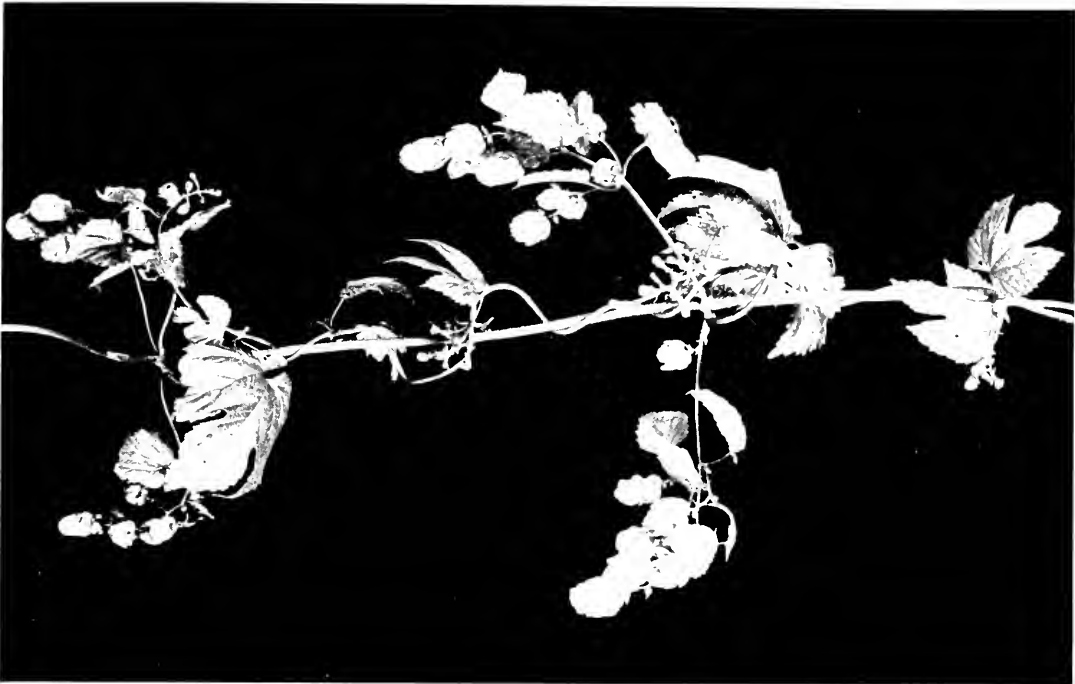


Fig. 2.

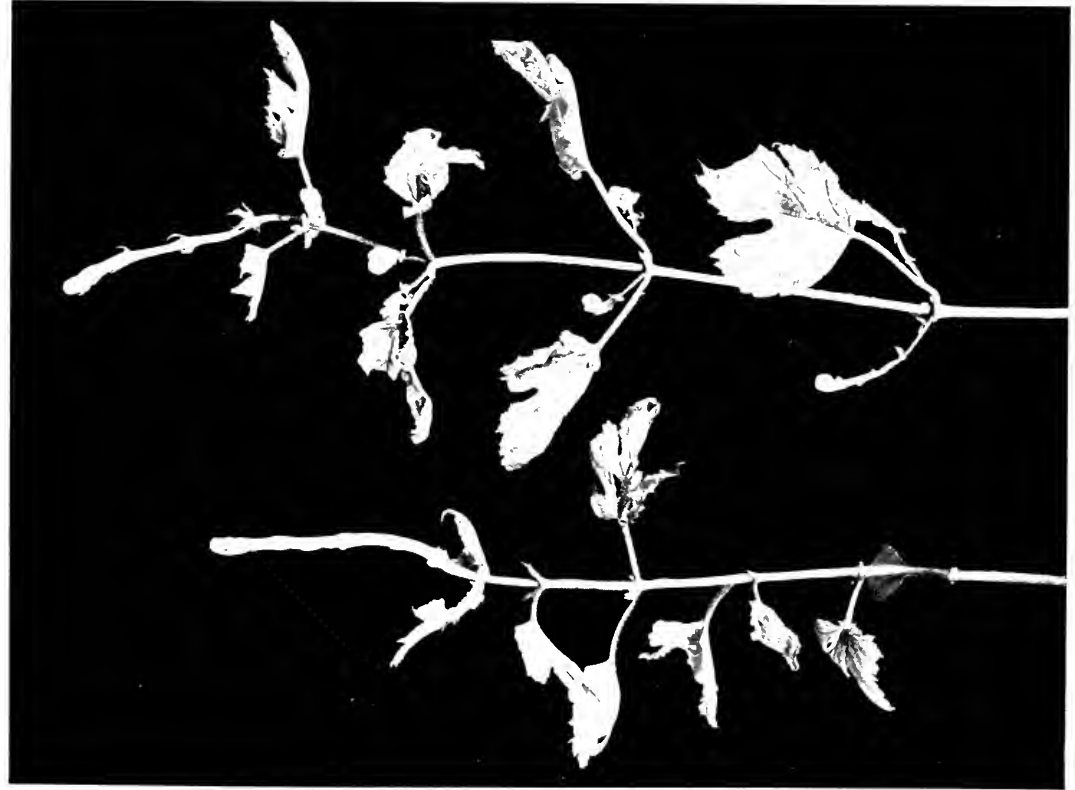


Fig. 1.



"Blätter kleiner, Fruchtstände etwa um die Hälfte kürzer, nur 1–1,5 cm. lang. Schuppen zum grössten Theile zugespitzt, etwas behaart, an der Spitze roth werdend.—Galizien." (Ascherson u. Graebner, *Syn. d. mittl-eur. Fl.* iv. 597 (1908–13)¹.)

SUMMARY.

1. The wild species *H. Lupulus* is composed of a number of forms with distinctive morphological and physiological characters.

2. Forms similar morphologically (for the characters taken) possess distinctive physiological characters (e.g., immunity from, or degrees of susceptibility to, mildew).

EXPLANATION OF PLATE XXV.

Fig. 1. Laterals of a seedling (of the wild hop) very susceptible to mildew; the inflorescences have been arrested in development.

Fig. 2. Intertwined laterals of two adjacent hop plants one susceptible to, the other immune from, mildew (see p. 260).

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¹ We are indebted to Mr E. G. Baker for this information.



MALE-STERILITY IN FLAX, SUBJECT TO TWO TYPES OF SEGREGATION.

BY W. BATESON, M.A., F.R.S.

AND MISS A. E. GAIRDNER,

Of the John Innes Horticultural Institution.

(With Plate XXVI.)

IN 1912 a single plant was noticed in a patch of *Linum grandiflorum* sown in our border of annuals. It was remarkable as having a blue flower and procumbent habit, whereas *L. grandiflorum* is deep crimson and erect. In its low stature the new plant somewhat resembles the various kinds of flax cultivated for oil in many countries. Several of these oil-flaxes have in subsequent years been grown here, but we had none in 1912, which was indeed the first year in which any form of *L. usitatissimum* was sown in this garden. All the flaxes cultivated, whether for fibre or oil, are included under that specific name. The new plant, which we shall here call the "procumbent," is also evidently a true *usitatissimum*, though in being procumbent it differs from any variety which we have seen. Obviously it has no connexion with *grandiflorum*, which is a very distinct species. We have no surmise as to what its origin may have been, but somehow a stray seed from which it arose must have got mixed with the *grandiflorum*.

Since in 1912 experiments on flax were begun with various objects the appearance of the procumbent was a matter of interest, and its seeds were collected. Whether the flowers had been covered is not recorded. Probably they were, but the point is of little importance, for only a small percentage of crossing occurs in *usitatissimum*. The procumbent bred true from the first and has continued true in each year since, except that a naturally cross-bred plant appeared once in a row raised from unprotected seed, as may happen with any flax.

The new form differs from any other flaxes that we know in the following respects.

1. It is procumbent during growth, branching much from the base, and the stems reach about 2 ft. in length, *lying at first flat on*

the ground, turning upward as flowering begins, and finally standing more or less erect.

2. The style is *very pale* in colour, and when the petals of an opening flower are pulled off it projects well above the sepals, which are perhaps slightly shorter than those of ordinary flaxes. But like other forms of *usitatissimum* the variety is definitely homostyled, the tops of the anthers just reaching beyond that of the stigma.
3. It is *very late in flowering*, about 10 days later than any other variety that we have.

In other respects there is nothing special to note. The capsule and seeds are of the ordinary size, not large as those of our oil-flaxes are.

The first crosses were made in 1916 by Miss M. Michell of Cape Town, who fertilised the procumbent with pollen from a tall white-flowered fibre-flax. The object of this cross was to study the genetics of height. Though from the extraordinary uniformity in height characteristic of *pure lines* of flaxes these plants seem well adapted for such work, the distribution of height in F_2 is complicated, all intergrades occurring, with indications of segregation so imperfect that useful results could only be obtained by measurements on a very large scale continued through several generations. Much work of this kind has been carried out on which we may publish a report later, but at present it must suffice to say that though segregation in respect of height occurs, and though the parental types, both procumbent and tall, reappear in F_2 , they are rare, and the height-curves of these families show no obvious dimorphism.

The purpose of the present paper is to give the facts respecting the behaviour of a *male-sterile* form which appeared in F_2 in 1918. F_1 is erect and intermediate in height, and in colour also (as T. Tammes found¹ in crosses between blue and white flaxes, and as we have also often seen in other cases). In F_2 Miss H. Garlick, who was then in charge of these experiments, observed certain plants, both blue, white and intermediate in colour, which had flowers with reduced petals, as a rule scarcely opening at all. In these flowers the anthers are more or less completely aborted. A row of such plants growing beside a row of normally flowered flaxes is shown on Pl. XXVI, together with photographs of drawings of the normal and of the abnormal flowers in various stages.

¹ Tammes, T., *Rec. Trav. bot. Néerl.*, 1911, viii, pp. 264-5.

Varieties with aborted anthers are familiar in a great number of plants. Some, as for example that of the Sweet Pea, are quite sharply defined, others, as for instance that studied by Miss Pellew in *Campylocarpus carpatia* may exist in many intergrading forms. As in the Caryophyllaceae and Labiatae, such flowers may coexist in various grades on the same plant, and may even be associated with normal hermaphrodite flowers. In these and other Natural Orders flowers with aborted anthers are both by systematists and writers on genetics often referred to as females, and the species possessing them are called gynomonoeccious or gyno-dioecious as the case may be. It is not easy to apply any definition which will distinguish flowers or plants with aborted anthers from the normal female flowers of some dioecious species (e.g. *Lychnis*), but to avoid raising this theoretical question we propose to follow the usage of some American authors and call them male-steriles. In these flaxes the sterility of the anthers is nearly but not quite complete. No grades of plants were recognized beyond the ordinary hermaphrodites and the male-steriles, but anthers of the steriles occasionally reach a degree of development sufficiently complete to produce a little good pollen. Flowers with this low degree of male-fertility may be found sporadically, as it seems, on any male-sterile plant. From their pollen a few seeds have been obtained in self-fertilisation which gave rise again to male-steriles only. No degree of male-sterility was ever observed in the flowers of ordinary flaxes. In the breeding work it was not thought necessary to emasculate the male-sterile flowers, and in only one mating (Expt. 5) is there reason to suppose that disturbance was caused by their pollen.

In previous experiments on the genetics of male-sterility the male-steriles were introduced as an already recognized type. In our work they arose in F_2 from a cross between two fully hermaphrodite types. Subsequent experience proved that the new form was brought in by the pollen of the common flax, and that the procumbent is genetically hermaphrodite on both male and female sides. Twenty-four fibre-flax plants of various kinds (Expts. 6—10) tested by using their pollen on male-steriles, gave in all 640 plants, all male steriles. To these 24 which gave a uniform result may be added the white plant, from the male side of which the original F_2 family containing male-steriles was derived, and a tall blue plant on similar grounds (Expts. 1 and 2).

One tall plant (Expt. 11) used as male on a male-sterile gave a hermaphrodite. If authentic, this constitutes a single exception to the rule that the pollen of normal flaxes carries the male-sterile only.

Whether it should be discarded as an error or not we cannot yet say. It came in a family containing only two plants, the other being a male-sterile.

From the evidence of these 26 plants we must conclude that the fibre-flaxes in general, perhaps always, are heterozygous in respect of the male-sterile allelomorph, and that in segregation this allelomorph is relegated to the male side.

As regards oil-flaxes we have only preliminary indications and can make no statement as yet.

The procumbent itself is clearly hermaphrodite in genetical composition on both male and female sides. The male side was tested as follows. Tall \times procumbent (Expt. 3) gave from 3 F_1 plants 559 all \varnothing in F_2 ; white \times procumbent similarly gave 157 \varnothing in F_2 (Expt. 4); also male-steriles fertilised by procumbents (3) gave 101 \varnothing , and also 2 male-steriles (Expt. 5) which may safely be assumed to have arisen by self-fertilisation, the mother-plant not having been emasculated.

But when the procumbent is used as mother and fertilised with pollen from a fibre-flax, F_1 is a normal hermaphrodite, and in F_2 the male-steriles appear as 1 in 4. It is proved therefore that the female side of the procumbent must in some way be different in constitution from the female side of the ordinary flaxes. In heterozygosis with the female of the procumbent the dominant factor for anther-development passes with its negative allelomorph to both male and female organs of the offspring, thus producing an ordinary Mendelian result, but when the same negative is in heterozygosis with the female side of the common flax, it passes wholly to the pollen, evidently segregating not later than the constitution of the sexual organs. The ordinary flax, though heterozygous, is thus able to breed true just as *Begonia Davisii* does for singleness (though heterozygous for doubleness) and as the various *Oenotheras* investigated by Renner may do, though heterozygous for several complexes.

In connexion with this example the somewhat cognate evidence discovered by Miss Pellew in *Campanula carpatica* should be recalled. There also very similar plants were shown to possess distinct types of segregation in respect of the same negative allelomorph. The case of the flaxes differs from that of the *Campanula*, for in that example the plants in which both allelomorphs went to both sexual sides showed an irregular distribution, whereas here they follow a normal Mendelian system. It will be interesting to see whether a cytological basis for these phenomena can be detected.

Attempts to use the male-steriles *as males* in crossing have hitherto failed, the pollen produced by them being very small in amount.

Much interest would attach to the genetics of plants made in such a way that the male-sterility was brought from the *maternal* side into combination with one or other of the hermaphrodite factors introduced from the paternal side. Various possibilities are thus opened up. On these questions we have as yet no sufficient evidence, Expt. 19 being the only one bearing on the point. There the hermaphrodite element was that of the female side of procumbent, and it was brought in from the male side of a plant homozygous in F_3 or a homozygous F_2 . Tried on a male-sterile it gave 6 male-steriles and 1 ♂. That it should have given the ♂ is worth noting, but work on a large scale is required to explore the many alternative distributions which will possibly be encountered. Material for these investigations is being prepared.

Plants in which the distribution of factors differs on the two sexual sides of the same plant now form such a prominent subject of genetical consideration that some simple terms are required to facilitate discussion. We suggest that in the ordinary Mendelian distribution the segregation might be called *ambilateral*, effected on both sexual sides of the plant as distinguished from the *unilateral* segregation which carries the allelomorph wholly to one sexual side¹.

In other examples, e.g. the double-throwing single in *Matthiola*, we might speak of the segregation as partially unilateral. The exception mentioned above (Expt. 11) may indicate that here also the unilaterality may on occasion be partial, but unless the phenomenon recurs its significance is doubtful.

Details of Experiments.

P = Procumbent. MS = Male-sterile.

The "tall" strain is that first raised here by selection²; "Dark blue" is another raised since; "Dark blue tall" is another, now pure, raised by combination of the above.

Expt.		♂	MS
1.	From $P \times$ white, 3 F_1 plants gave in F_2	53	9
2.	„ $P \times$ tall, 4 „ „ „	308	100
	Totals ...	361	109
3.	From tall $\times P$ 3 F_1 plants gave in F_2	559	—
4.	„ white $\times P$ 3 „ „ „	157	—
	Total ...	716	—
5.	$MS \times P$		
	5 mothers \times 3 fathers gave ...	101	2
	The 2 MS resulting were doubtless due to self-fertilisation		

¹ *Proc. Roy. Soc.* 1920.

² *Journal of Genetics*, Vol. v. 1916, p. 199.

MS × various fibre flaxes.

Expt.		Parents used		Offspring	
		♀	♂	♀	<i>MS</i>
6.	<i>MS</i> × tall	15	16	—	402
7.	„ × dark blue tall	2	1	—	57
8.	„ × dark blue	5	3	—	72
9.	„ × white	5	3	—	77
10.	„ × Canadian fibre	1	1	—	32
Totals		28	24	—	640

11. In addition to these was the exceptional case in which *MS* × a tall gave 1 ♀ and 1 *MS*

F_2 plants from Expt. 2 were tested as follows :

Expt.		♀	<i>MS</i>
12.	Two ♀s selfed gave F_3	98	30
13.	Two <i>MS</i> × two sister ♀s (1 used in Expt. 12) gave proving that these ♀s were heterozygous.	14	12
14.	One <i>MS</i> × sister ♀ gave proving that this ♀ was homozygous.	41	—
15.	5 ♀s from Expt. 13 selfed gave	378	140
16.	4 ♀s from Expt. 5 selfed gave	298	87
17.	4 <i>MS</i> × sister ♀s gave	58	58
18.	2 ♀s of complex origin (derived from $P \varphi$) gave ...	43	25

Adding families derived from $P \varphi$, which are expected on selfing to give 3 : 1. There are

Expt.	♀	<i>MS</i>
1.	53	9
2.	308	100
12.	98	30
15.	378	140
16.	298	87
18.	43	25
Totals ...	1178	391

Adding those expected to give 1 : 1

Expt.	♀	<i>MS</i>
13.	14	12
17.	58	58
Totals ...	72	70

Expt.

19. Case mentioned, p. 273.

<i>MS</i> × ♀ from Expt. 14 [viz. a plant which had received <i>MS</i> from maternal side and hermaphrodite factor from the paternal side] gave	♀	<i>MS</i>
	1	6



Fig. 1.



Fig. 2.



Fig. 3.



Fig. 4.



Fig. 5.



Fig. 6.



Fig. 7.



Fig. 8.

EXPLANATION OF PLATE XXVI.

- Fig. 1. A row of male-sterile plants (left) growing beside a row of normal plants (right).
- Figs. 2—8. Drawings of flowers with petals and sepals removed ; Figs. 2—4 and 6 from blue-flowered plants ; Figs. 5, 7 and 8 from whites.
- Fig. 2. Normal just before opening.
- Fig. 3. Same later, anthers dropped.
- Fig. 4. Male-sterile, unopened flower, the usual condition.
- Fig. 5. Rarer condition of male-sterile, unopened flower. Stamens more developed, occasionally bearing some pollen.
- Figs. 6—8. Later stages of male-steriles. Anthers shrivelled but persisting.



THE INHERITANCE OF WING-COLOUR IN LEPIDOPTERA.

VI. *DIAPHORA MENDICA* CL. AND VAR. *RUSTICA* HB.

By H. ONSLOW,
Trinity College, Cambridge.

(With Ten Text-figures and Plate XXVII.)

THE inheritance of several melanic varieties has been dealt with in some recent papers, the melanic character being found as a rule dominant to the type form. In the case of *Odontopera bidentata* and of *Abraxas grossulariata* (var. *varleyata*), the black variety behaves as a recessive. The first insect has no doubt a true melanic form, but in the case of *varleyata* the existence of the white collar at the base of the wings suggests a pattern factor rather than melanism. Melanism as a rule takes the form of a general suffusion with black or very dark scales, the pattern being sometimes so completely obscured that the insect appears uniformly black.

The subject of this paper, *D. mendica* (The Muslin Moth), cannot be included strictly among melanics. In England this insect is sexually dimorphic, the male being dark brown or black, with a number of distinct black spots of very variable size, the female pure white with similar spots (see Nos. 1, 2 and 11, 12, Pl. XXVII). In Ireland, however, there is a race, the males of which are nearly as pale as the females, but of a creamy shade rather than dead white (see Nos. 9 and 10, Pl. XXVII). This race, var. *rustica* Hb., is also found in the Caucasus, Hungary, Roumania, Silesia and Armenia. Experiments have already been carried out in crossing the variety with the type form, by Caradja¹, Standfuss², Tutt³, Adkin⁴ and recently by Cockayne⁵. Tutt found, as did Caradja,

¹ *Societas entomologica*, Zurich, Vol. ix. No. 7, p. 49, 1894—5, and Vol. x. No. 7, p. 49, 1895—6.

² Standfuss, *Handbuch paläarkt. Gross-Schmetterlinge*, 1896, p. 223.

³ Tutt, J. W., *British Lepidoptera*, Vol. v. p. 45.

⁴ Adkin, R., *Entomologist*, Vol. xxx. p. 206, 1897.

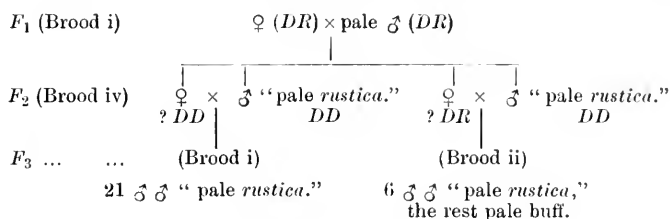
⁵ Cockayne, E. A., *Ent. Record*, Vol. xxxi. No. 6, p. 101, June 15, 1919.

that the males of the F_1 generation were a little darker than *rustica*. Adkin described the hybrid males as dusky white, and Standfuss, who obtained his pupae from Caradja, bred 17 F_1 ♂♂, the darkest of which was much lighter than the lightest type. Caradja classified the F_1 hybrids under the names of var. *standfussi* (intermediate between dark grey and milk white), var. *mus* (darker grey but lighter than type), var. *clara* (pale dirty yellow), and var. *mixta* (pale as *clara*, but heavily spotted). Nevertheless, 20 per cent. of the males could not be classified in any of these categories. All these authors, however, agree in finding the F_1 ♂♂ but little darker than those of var. *rustica*.

The fullest details are recorded by Cockayne, and he concludes that "the results show no segregation of the dark brown colour of the type form takes place, either in F_2 or F_3 generations;.....even with the small numbers bred I think it safe to say that the pale colour of var. *rustica*, and the dark brown of the type do not behave as Mendelian unit characters." The present writer does not consider that sufficient evidence is advanced to justify these conclusions, and, moreover, the experiments recorded later suggest that segregation does take place, though it is partly obscured by modifying genes which tend to make the variation appear continuous. The 46 F_1 ♂♂ recorded by Cockayne vary from creamy brown to the same pale colour as *rustica*. In the F_2 generation, which in the event of segregation should approximately contain 3 pale or buff insects to every black one, only 4 ♂♂ are recorded, and one of these was described as a dark intermediate. Moreover, from the data given, all the F_3 generation came from matings of the form $DD \times DD$ or $DD \times DR$ (where D stands for the imperfectly dominant factor for *rustica* and R for the factor of the recessive black type form). This may be more clearly seen from the pedigree given below. Only two F_3 broods are recorded, namely (i) and (ii), the male parents of which came from the F_2 generation, and are described as "pale *rustica*," thereby almost certainly having the constitution DD . The two female parents came from the same F_2 family as the male parents, but being of course white they might have had any constitution, DD , DR or RR . Since, however, the 21 ♂♂ recorded in brood (i) were as pale or rather paler than *rustica* (one was said to be like var. *mixta*), the ♀ must have been DD or at least DR . In brood (ii), 6 of the ♂♂ recorded were as pale as *rustica*, and the others (number not mentioned) were a pale creamy brown. The male parent of this brood was, as has been pointed out, DD , and therefore the female parent must have been DR , because the male offspring were, as would be expected, partly *rustica* and partly buff (DD

and DR). Thus we see that in the F_3 generation no type insects could be expected to appear in any circumstances. Moreover, of the 4 ♂♂ of the F_2 generation, at most one should have been a type. Surely this is not sufficient evidence on which to deny the occurrence of segregation!

Table showing the Relationship of the Insects bred by E. A. Cockayne.



Experimental.

The strain of *rustica* used in the following experiments came from Ireland (Co. Tyrone), and the type insects came either from Bexley, Kent, or from Cambridge, where they were attracted by caged females. The work was commenced in 1915, but owing to the disease which has been recorded by every observer, the stock nearly died out on more than one occasion. This disease, which only attacks the full-grown larvae, is said by Cockayne to show no signs of being transmitted through the ova, though as long as the majority of the families are affected, this must be a difficult point to decide. Cockayne moreover suggests that the infection may be carried by the food, which was in his case nettles, since he observed that neither the sterilisation of the sleeves nor the cages prevented it.

At the commencement of these experiments, the larvae were fed on plaintains grown in large earthenware pots. These proved so cumbersome, and the incidence of the disease so severe, that in the following season the young larvae were put in glass cylinders filled with willow. All the cylinders were sterilised, and in order to prevent the spread of infection, each brood was placed upon fresh clean paper while renewing the food-plant, and the hands, brushes and everything used in feeding were also sterilised. With these precautions, unless the disease was transmitted through the ova, or carried by the food-plant, little infection should have taken place. Nevertheless, some families developed the disease, but at the same time it was possible to keep others completely free from it, so that nearly all the pupae would emerge. In other cases the disease would only appear at the last moment when the larvae were beginning to pupate.

In these circumstances a large number would pupate successfully, but next year only from 25 to 50 per cent. would emerge. When the disease appeared some time before pupation, the case was usually hopeless, and the family was thrown away to prevent further infection. From the limp and disintegrating look of the sick larvae the disease appeared as if it might be due to a proteolytic bacterium, but smears of the blood failed to show any definite organism. It was possible, however, that the examination was not made at a sufficiently early stage.

The F_1 ♂♂ hybrids from the first cross of *rustica* × type, like those of previous observers, varied from cream to a dark buff (see Nos. 3 to 7, Pl. XXVII), but were sometimes milk white like var. *rustica*, or white with a fleck or two of grey, especially on the hind wings (see No. 8, Pl. XXVII), but the range of colour was considerable. In order to classify these intermediate forms for analysis, it was necessary to give them definite colour values, which was done by means of the tintometer in the manner previously described¹. To match the various shades of grey it required approximately the same number of units of blue, red and yellow. In the case of the dark insects orange-red predominated, and in the case of the cream and buff coloured insects, orange-yellow. The following table gives the colour values of some characteristic insects:

Insect	Black	Red	Orange	Yellow
'18 W ♂ 3 (type)	6.4	0.4	0.6	—
'18 W ♂ 2 (type)	5.2	—	0.8	—
'19 I ♂ 15 (F_1 hybrid)	2.5	—	0.5	0.2
'19 K ♂ 14 (F_1 hybrid)	1.5	—	0.4	0.1
'16 D ♂ 2 (<i>rustica</i>)	0.3	—	0.3	0.3
'16 D ♂ 6 (<i>rustica</i>)	0.2	—	0.3	0.5
'16 D ♂ 7 (<i>rustica</i>)	0.1	—	0.5	0.6
Typical ♀♀	0.4	—	—	0.2

Unfortunately there were a certain number of insects which had light veins (cf. No. 6, Pl. XXVII) and others which showed a central area paler than the periphery (cf. No. 3, Pl. XXVII). It at first appeared very difficult to give such insects a value which would represent the mean colour, but after several attempts the following method was adopted. One or both wings were removed from the body and mounted at the centre of a large cork, which was then fitted to the shaft of an electric motor. On revolving the motor at a sufficient speed, the markings on the wings blend, as on the colour-wheel, into a uniform field, which can be measured by the tintometer in the usual way.

From the values in the table above it is clear that the figures for orange and yellow are small enough to be insignificant, and since their

¹ Onslow, H., *Journal of Genetics*, Vol. VIII, p. 225, September, 1919.

inclusion would greatly complicate the record, they have been omitted, the black values alone being given. From these figures a number of curves have been constructed, showing the distribution and percentage distribution of the colour values, on the system previously adopted, to illustrate the variation of the insects in the principal families of each type of mating. The colours of the parents are shown by arrows, and in addition to the curves, tables have been given which include every insect bred. For simplicity, the male insects in these tables had to be classified into three groups. The black group, consisting of insects like the wild type, and the white or cream coloured group of insects like var. *rustica*, obviously represent the *DD* and *RR* classes, but the *DR* class of insects presents a difficulty. It includes all the grey or buff coloured males of the F_1 generation, and as these have been called var. *standfussi*, that name might have served to designate the whole class. The name is, however, misleading, because whereas buff or grey males are always intended, the name should include every insect of the *DR* class, some of which, it has been pointed out, are so pale as to be indistinguishable from pure *rustica* (see families '16 A and '19 B in Fig. 1). Thus

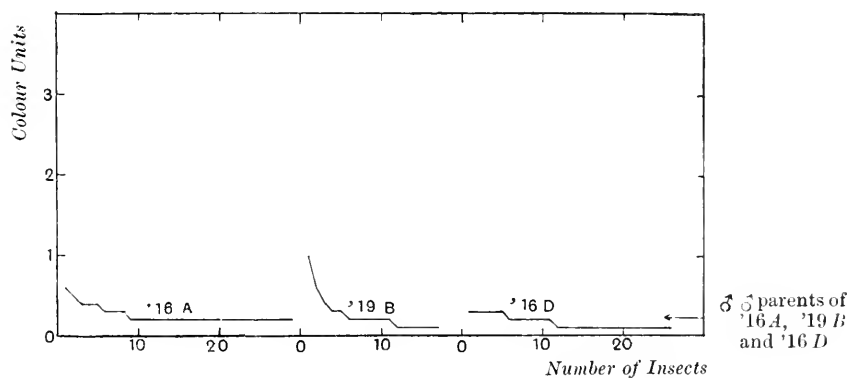


Fig. 1 (cf. Fig. 2). Curve showing the distribution of the black values of the ♂♂ in family '16 D bred from *rustica* ♀ × *rustica* ♂; also the values of the ♂♂ in the two families '16 A and '19 B bred from (F_1) × *rustica*.

there may be some males, which, though they appear to be pure *rustica*, are genetically heterozygous for the black pigment, the white form being completely dominant. For this reason, the *DD* class has been called "pure *rustica*" to distinguish it from the *DR* class, called "*rustica* and *standfussi*," which includes both *standfussi* and the heterozygous males indistinguishable from *rustica*. It was also necessary that the classes

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should correspond to definite portions of the colour scale, and as far as possible the following values have been taken :

Class of insect	Black colour values
"Pure <i>rustica</i> " (<i>DD</i>) ...	0.0—0.5
<i>rustica</i> and <i>standfussi</i> (<i>DR</i>)	0.5—4.0
Type (<i>RR</i>)	4.0—6.0

In the table (p. 286) which shows the F_2 generation, the range of colours is not quite the same, the whole scale being slightly shifted towards the black.

The white variety is, as has been said, usually imperfectly dominant but sometimes the dominance is complete. The heterozygous males are grey or buff, and in the F_2 and other generations, in spite of a considerable variation, the accompanying curves, constructed from the colour values, show that the white and black homozygous insects tend to segregate in accordance with the ordinary Mendelian ratios. The variation of the colour is most probably caused by the presence of a modifying gene or genes, in much the same way as the very variable radiation of the black

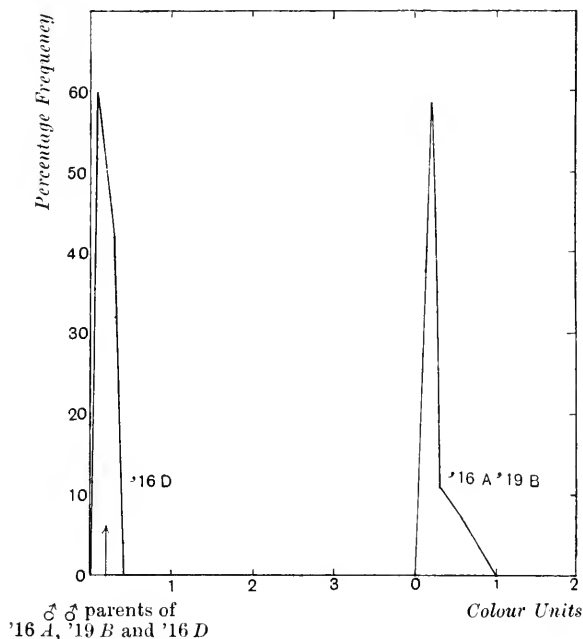


Fig. 2 (cf. Fig. 1). Diagram showing the percentage frequency of the black values of the pure *rustica* ♂♂ in the last figure; as well as of the ♂♂ in the two (F_1) \times *rustica* families '16 A and '19 B which have been combined.

forms of the allied species *Spilosoma lubricipeda*, the Heligoland variety *zatima* Cr., and var. *intermedia* Standf., the genetics of which have been worked out by Federley¹.

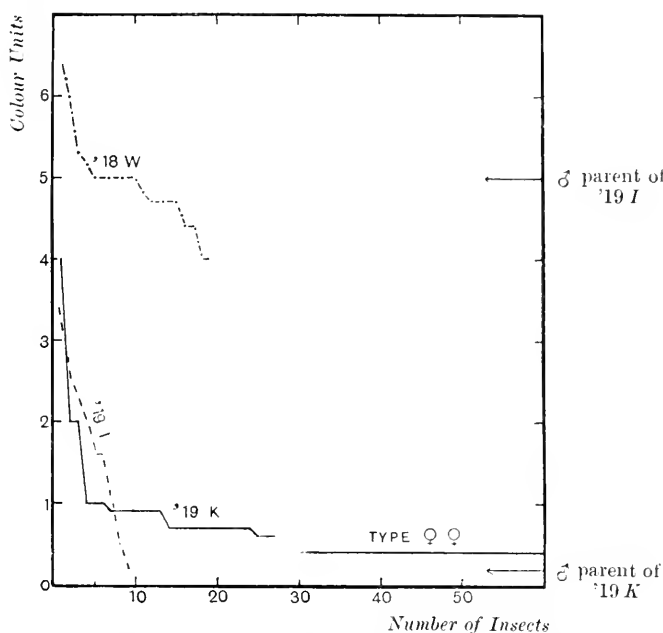


Fig. 3 (cf. Fig. 4). Curves showing the distribution of the black values of the ♂♂, from a wild type family, '18 W'; as well as the values for the ♂♂ in the two F_1 families, '19 I and K. The value for ♀♀ of any breeding is given by the line on the right-hand side.

From matings of *rustica* × *rustica* only *rustica* were obtained. Reference to Figs. 1 and 2 (Family '16 D) shows that the black values of these "pure *rustica*" all fall round 0.2. Similarly, matings between wild type insects gave nothing but dark males, the colour of which varies considerably within certain limits. The extent of these may be clearly seen from family '18 W, Figs. 3 and 4.

The colour variation of several typical F_1 hybrids is shown by families '19 K and '19 I (see Figs. 3 and 4, also Nos. 3 to 7, Pl. XXVII). These hybrids appear to be the same whether the male parent is white or black. Standfuss and Caradja consider that the male has more influence in determining the appearance of the offspring than the female, but this is probably due to the comparatively small numbers they obtained. In

¹ Federley, H., *Hereditas*, Vol. 1, p. 221, 1920.

rustica × *rustica*.[*DD* × *DD*].

Family	Imagines			Female
	Male			
	"Pure <i>rustica</i> " (<i>DD</i>)	<i>rustica</i> and <i>standfussi</i> (<i>DR</i>)	Type (<i>RR</i>)	
'16 <i>D</i>	28	—	—	21
'17 <i>C</i>	2	—	—	2
'18 <i>E</i>	5	—	—	5
Totals	35	—	—	28

the following table the F_1 hybrid ♂♂ have all been included under the heading "*rustica* and *standfussi*." Many of these ♂♂ were pale, but as a rule they were not quite so pale as "pure *rustica*," or the *DR* insects of families '16 *A* and '19 *B* (see Fig. 1). The very dark ♂ (Fig. 3) with a value of 4.0 is so black that it is probably a type insect included by mistake. The average value for these F_1 insects is seen from Fig. 4 to be not much above 1.0, so that it may be inferred the dominance of *rustica* is nearly complete.

rustica × *Type*.[*DD* × *RR*].

		Imagines			
		Male			Female
Family	Female × Male	"Pure <i>rustica</i> " (<i>DD</i>)	<i>rustica</i> and <i>standfussi</i> (<i>DR</i>)	Type (<i>RR</i>)	
'16 <i>G</i>	<i>rustica</i> × type	—	7	—	11
'16 <i>H</i>	" × "	—	1	—	2
'16 <i>F</i>	type × <i>rustica</i>	—	2	—	4
'16 —	Ova from Mr L. Newman	—	3	—	1
'17 <i>F</i>	<i>rustica</i> × type	—	1	—	3
'17 <i>I</i>	type × <i>rustica</i>	—	1	—	3
'19 <i>F'</i>	" × "	—	2	—	4
'19 <i>K</i>	" × "	—	27	—	42
'19 <i>I</i>	<i>rustica</i> × type	—	9	—	13
Totals ...			53	—	83

The F_2 generation, obtained by crossing two F_1 insects, might be expected to give approximately *rustica*, *standfussi* and type, in the ratio 1:2:1. As the table on p. 286 shows, this appears to be the case, except that the *DD* class is rather too large, owing of course to the fact that it must contain a few white insects, indistinguishable from *rustica*, which are genetically heterozygous (*DR*). In these circumstances the *DR* class only contains *standfussi*; and the *DD* class can only be called *rustica*. Although the totals approach the expectation, the numbers in the individual families seem to vary widely, and the fact that the ratio is so

closely realised must be due to there being sufficient numbers to give an average. A glance at Fig. 6 shows that the curve of the combined families divides fairly sharply into three classes, the *DR* class being about twice as numerous as the other two. The individual families, however, which are seen in Fig. 5, show wide divergences. This is probably due

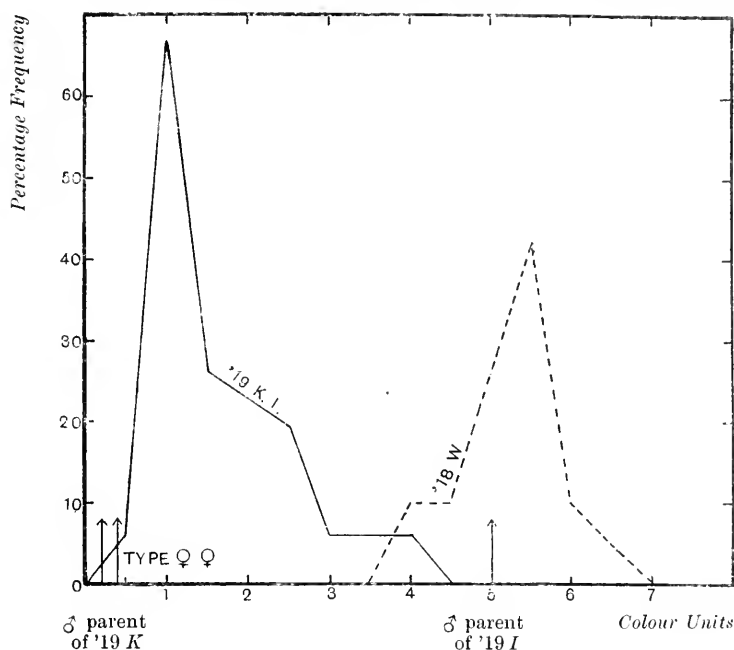


Fig. 4 (cf. Fig. 3). Diagram showing the percentage frequency of the black values of the type ♂♂ in the last figure. The two F_1 families have been combined.

to the variation in the colour of the parents, i.e. to the modifying genes which shift the range of colour of single families up or down the scale. Family '20 *E* is, for instance, shifted towards the dark end of the scale, whereas family '20 *B* is shifted in the other direction, and has, moreover, much the palest male parent. If the curve is considered as a whole, the classes are all a shade darker than the values given on p. 282; for instance the *DD* class of "pure *rustica*" extends as far as the black value 1.0. The extracted type males are many of them very dark, some being like No. 2, Pl. XXVII, black rather than brown, and darker than the ordinary wild male. The extracted *rustica* are like the Irish race, but some have a small patch of light grey scales on the milky ground somewhat lighter than No. 8, Pl. XXVII, and others are more heavily spotted than usual, with a black streak down the costa (No. 10, Pl. XXVII).

$F_1 \times F_1.$
 $[DR \times DR].$

Family	F ₂ Imagines			Female
	Male		Type (RR)	
	<i>rustica</i> (DD)	<i>standfussi</i> (DR)		
'17 D	3	—	—	8
'17 E	4	1	—	3
'17 G	—	—	—	2
'18 D	5	8	4	27
'20 A	7	15	17	29
'20 B	10	8	—	26
'20 C	2	8	—	10
'20 D	4	4	2	12
'20 E	7	13	14	37
'20 F	9	9	—	22
'20 G	2	11	3	13
'20 I	1	1	1	5
Totals ...	54 (31 %)	78 (45 %)	41 (24 %)	194
<i>Expectation...</i>	<i>43</i>	<i>86</i>	<i>43</i>	—

By pairing the F_1 hybrids back to type insects, two fairly distinct classes were obtained; insects as dark as type or darker with black values above 4.0, and intermediate insects with black values considerably below 4.0 sometimes even falling below 0.5. Reference to Figs. 7 to 10 will show how clearly these two forms segregate. In family '19 C (Fig. 7) there is a gap of over two colour units between the RR and the DR insects, and in family '18 A (Fig. 9) the gap is as large. In the other families segregation is scarcely less complete. There appears to be no difference in the colour of the offspring, whether the type insect is the male or the female parent.

$F_1 \times T_{type}.$					
$[DR \times RR].$					
		Imagines			
		Male			Female
Family	Female \times Male	"Pure rustica" (DD)	rustica and standfussi (DR)	Type (RR)	
'17 B	$F_1 \times \text{type}$	—	7	2	8
'18 B	$\text{type} \times F_1$	—	37	30	44
'18 A	$F_1 \times \text{type}$	—	21	23	42
'19 A	$\text{type} \times F_1$	—	11	15	40
'19 C	" \times "	—	17	18	30
'19 D	" \times "	—	32	41	89
'19 E	" \times "	—	5	5	16
'19 G	$F_1 \times \text{type}$	—	1	1	3
'19 H	$\text{type} \times F_1$	—	11	2	11
Totals	...	—	142 (51%)	137 (49%)	283
Expectation	...	—	139.5	139.5	

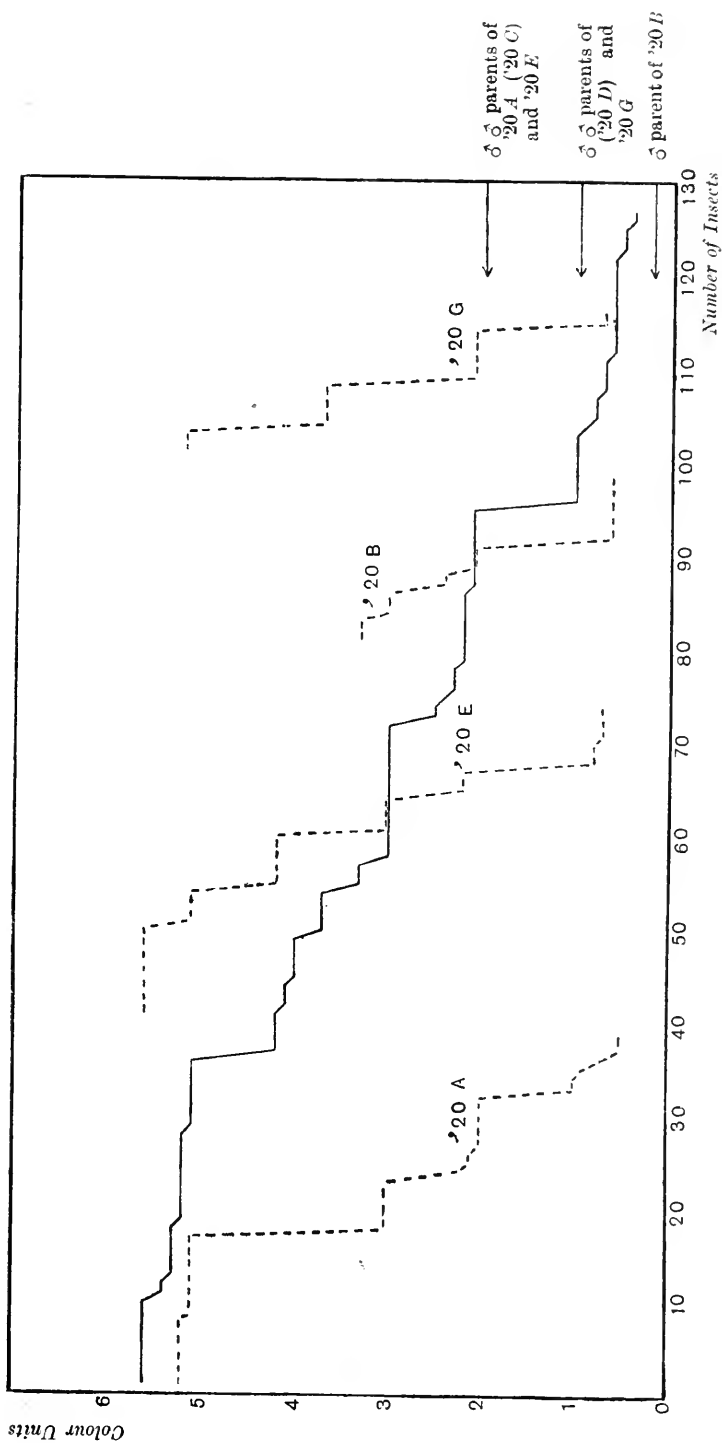


Fig. 5 (cf. Fig. 6). The distribution of the black values of the σ σ in most of the F_2 families in the last table is shown by the continuous black line. Dotted lines show the values of the σ σ in families 20 A, B, E and G superposed on the first curve.

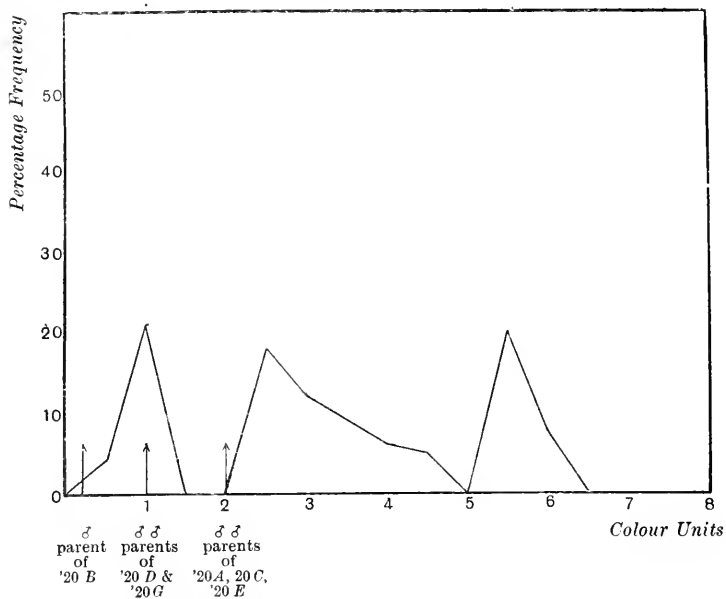


Fig. 6 (cf. Fig. 5). Diagram showing the percentage frequency of the black values of the ♂♂ shown in the last figure, illustrating the segregation of the three classes *DD*, *DR* and *RR*.

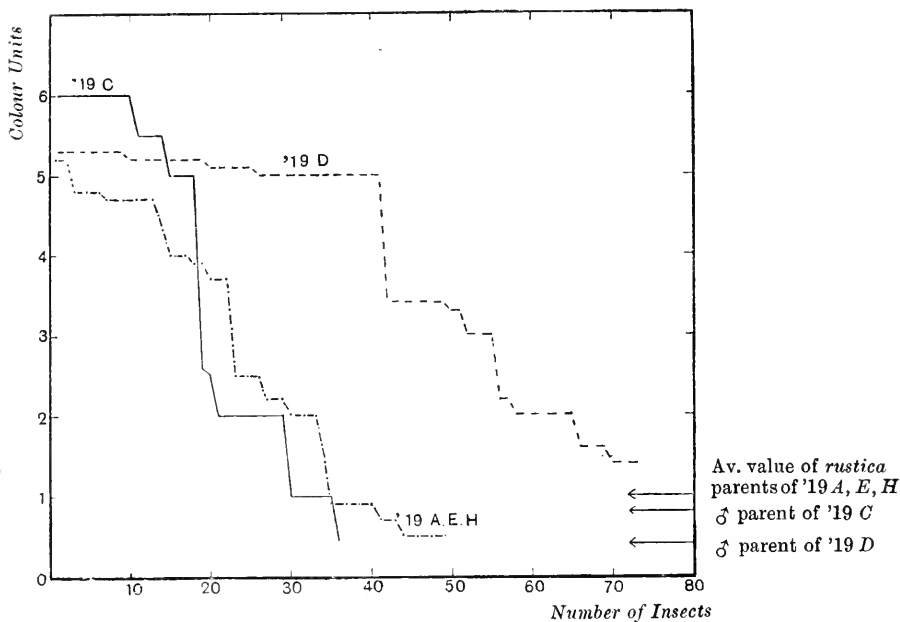
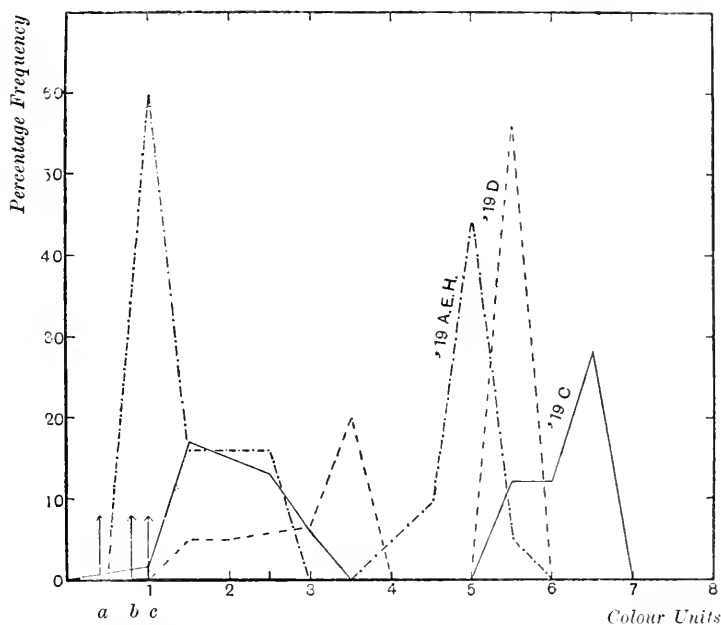


Fig. 7 (cf. Fig. 8). Curve showing the distribution of the black values of the ♂♂ in five families of the cross (F_1) \times type.

When the F_1 hybrids were mated back to pure *rustica*, most of the offspring were as pale as the *rustica* parent, and a few were slightly tinged or flecked with buff or grey, as may be seen from the colour values in families '16 A and '19 B, Figs. 1 and 2. There should of course be equal numbers of "pure *rustica*" DD and DR , but owing to the impossibility of separating the two forms of *rustica* except by breeding



a ♂♂ parents of '19 D. b ♂ parent of '19 C.
c Av. value of *rustica* ♂♂ parents of '19 A, E, H.

Fig. 8 (cf. Fig. 7). Diagram showing the percentage frequency of the black values of the ♂♂, in the families of the cross (F_1) × type shown in the last figure.

$F_1 \times rustica$.

[$DR \times DD$].

Family	Female × Male	Imagines	
		Male	Female
		<i>rustica</i> and <i>standfussi</i> (DD and DR)	Type (RR)
'16 A	$F_1 \times rustica$	36	—
'17 A	„ × „	3	—
'17 H	„ × „	8	—
'17 K	$rustica \times F_1$	10	—
'18 C	$F_1 \times rustica$	1	—
'19 B	$rustica \times F_1$	28	—
Totals	...	86	—
			60

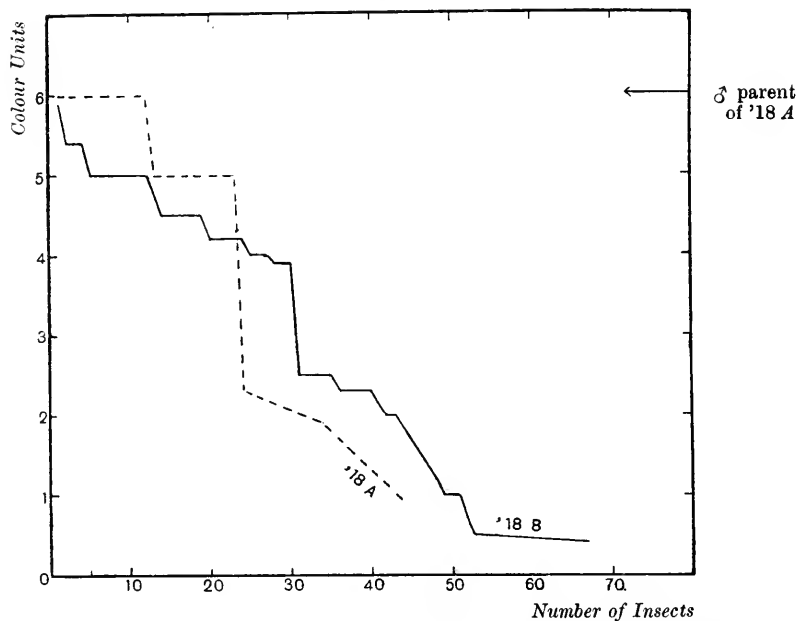


Fig. 9 (cf. Fig. 10). Curves showing the distribution of the black values of the ♂♂ in two families of the cross (F_1) \times type. Note the two distinct plateaux in '18 B.

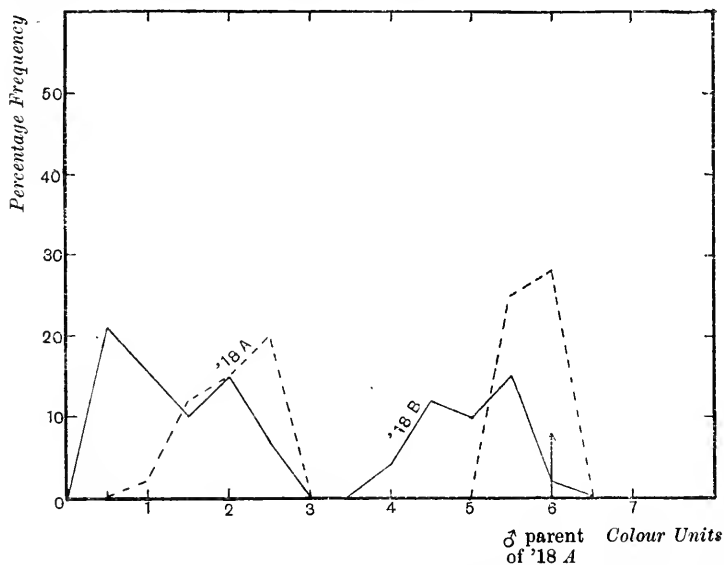


Fig. 10 (cf. Fig. 9). Diagrams showing the percentage frequency of the black values of the ♂♂ in the two families of the cross (F_1) \times type shown in the last figure.

experiments, they have all been placed together in the column "*rustica* and *standfussi*" (*DD* and *DR*) and the variation of colour must be judged by reference to the curves.

There is one more point of some interest. Both Tutt and Caradja consider that *rustica* is phylogenetically the older form, and in this Cockayne agrees, believing that a black race arising in the centre of Europe has spread in all directions replacing the old white race everywhere except in the extreme periphery of its habitat, as in Ireland and the Caucasus. In the light of present knowledge this seems to be undoubtedly correct, for if evolution has taken place largely, if not entirely, by the loss of factors, it is more probable that the white race *rustica* lost a factor which inhibited the formation of black pigment in the male, than that the black race lost the power to produce black pigment. If the latter alternative were true, the white insect produced would be in the nature of an albino, and as is invariably the case with albinism in other animals, it would be recessive to the coloured form. It has, however, been shown that the white race is almost completely dominant to the black race, that is to say, it behaves as a "dominant white," like the English rabbit. Now dominant whites are supposed to contain a factor inhibiting pigment production; and extracts from the skins of English rabbits have been shown to contain an inhibitor capable of preventing the production of pigment by the enzymes from the skins of black and other coloured rabbits¹, whereas extracts from the skins of albinos fail to do so. Thus the suggestion that the dominant form is phylogenetically the older is probably correct.

CONCLUSIONS.

1. It is contended that the evidence advanced by Cockayne is not sufficient to deny segregation in the Mendelian sense, in crosses between *D. mendica* and its white variety *rustica*.

2. The experiments reported show that in the F_1 generation the males are not much deeper in colour than "pure *rustica*," so that this form may be considered dominant to a great extent over the type; in fact, some heterozygous insects are indistinguishable from *rustica*.

3. The great variation in the buff coloured hybrids is probably due to the effects of modifying genes. The colour of these buff insects as well as that of the others was measured in the tintometer. The construction

¹ Onslow, H., *Roy. Soc. Proc. B*, Vol. LXXXIX, p. 36, 1915.

of distribution curves in the manner previously described enables the segregation of these variable insects to be followed without difficulty.

4. Segregation is found to take place in the F_2 generation, the pure *rustica* and the black type males segregating from the heterozygous buff coloured insects in an approximately 1:2:1 ratio. Owing to the fact that some heterozygous males are indistinguishable from pure *rustica*, the latter class is found to be too numerous.

5. The crosses between the F_1 generation and type individuals also show very clear segregation in the males, there being equal numbers of type, and buff coloured or white insects.

6. The statement that var. *rustica* is phylogenetically the older race is supported by a consideration of what is known concerning the chemistry of black pigments.

I have to acknowledge my thanks to the British Association for defraying part of the expenses of this research by a grant of £25 during the year 1920, and I am also indebted to Professor Punnett for reading the manuscript. I am particularly grateful to Miss Helen Moodie for her care of the larvae and for her efforts to prevent the spread of infection while changing the food.

DESCRIPTION OF PLATE XXVII.

Diaphora mendica, var. *rustica* and hybrids. Natural size.

1. *D. mendica*. Typical wild English ♂ from Kent.
2. *D. mendica*. Black type F_2 ♂, extracted from var. *standfussi* (F_1).
3. Var. *standfussi*. Dark F_1 ♂ from cross *mendica* × *rustica*, showing pale central areas on fore wings.
Note the pale colour of the thorax and abdomen, a sure indication that the insect is heterozygous.
- 4, 5. Var. *standfussi*. Dark F_1 ♂ from cross *mendica* × *rustica*.
6. Var. *standfussi*. ♂ from cross F_1 × type, showing pale veining.
7. Var. *standfussi*. F_1 ♂ from cross *mendica* × *rustica*.
The colour of this insect, or a little darker, is about the usual shade of F_1 ♂.
8. Var. *standfussi*. ♂ from cross *rustica* × F_1 , showing patches of grey scales, which are not as a rule so dark.
9. Var. *rustica*. Typical white Irish ♂.
10. Var. *rustica*. White Irish ♂, showing black streak on costa.
11. Var. *rustica*. Irish ♀, showing black costa which appears in certain families, in which the black spots are often rather heavier than usual.
12. *D. mendica*. Typically English ♀ from Kent.

1



2



3



4



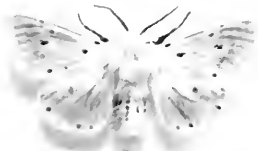
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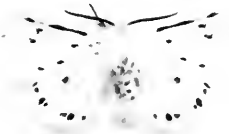
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12





THE INHERITANCE OF WING-COLOUR IN LEPIDOPTERA.

VII. MELANISM IN *HEMEROPHILA ABRUPTARIA* (VAR. *FUSCATA*, TUTT).

By H. ONSLOW,
Trinity College, Cambridge.

(With Plate XXVIII.)

THE inheritance of the melanic variety of *Hemerophila abruptaria* (The Waved Umber) has already been studied by T. H. Hamling¹ and E. Harris². Their experiments seem to show that the black form is dominant, but the ratio of type to melanic insects, obtained by them in the cross melanic (heterozygous for type) \times type, appears to suggest that the inheritance is not that of a simple Mendelian character. For this reason the breeding experiments recorded in the following pages were undertaken, and although they only serve to show that the surmise was mistaken, they are nevertheless perhaps worth recording.

One point of interest is that the variety *fuscata* appears to be confined to the environs of London, there being but one reference to its capture in the New Forest where it is exceedingly rare. In its distribution this variety is similar to some of the melanic forms already studied, in that it does not originate in any of the manufacturing districts of the North of England. The type insects used in these experiments came from Bexley, Kent (Nos. 1—6, Pl. XXVIII), and the melanic strain from Holloway, London (Nos. 7—12, Pl. XXVIII). In colour the latter was a deep chocolate brown, though the central band on the fore wings was not always completely obscured. The depth of colour of this band varies considerably, and appears to depend to some extent on the size and vigour of the larvae (see Nos. 11 and 12, Pl. XXVIII), but there is no difference in colour between a heterozygous melanic carrying type, and a pure homozygous black insect. Of the two sexes the male is usually the darker.

¹ Hamling, T. H., *Trans. City of London Ent. Soc.* 1905, p. 5.

² Harris, E., *Proc. Ent. Soc. London*, 1904, p. lxxii; and *ibid.* 1905, p. lxiii.

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The larvae were kept in the usual way in glass cylinders, and were fed on lilac throughout the summer. They feed rather slowly, but when ready to pupate, pieces of bark should be supplied, on which they can make their cocoons. If more than about twenty insects were placed to pupate in a single cylinder, a tendency was observed on the part of the larvae to congregate in a small area, so that when finished, their cocoons formed a continuous layer. As a consequence of this it was found that where insects were surrounded by other cocoons they were often unable to force their way out. It has been observed before that this species will produce a partial second brood when in captivity, though it must be rather unusual for an insect which as a rule hibernates in the pupal state, to do so in the larval state as well. Insects that remain as pupae during the winter begin to emerge as a rule in April or May, pairing and laying freely. Some of the larvae resulting from these eggs will if well fed pupate and emerge towards the end of July. These again pair and lay, giving rise to a second generation, which, if properly fed, and not kept too cold, often pupate before the end of the year. Such insects emerge in May of the following year, rather later than those insects which failed to emerge in July of the year before, and remained as pupae throughout the winter. Privet was used to feed the larvae after the lilac leaves had all fallen.

Very few records are to be found giving any useful information concerning the genetics of this melanic variety. Pearce¹ and Southey² both bred the melanic form, but their records are too deficient to be of much value. The most detailed experiments are those of Hamling and Harris already mentioned. Their data have been summarised by Tutt in *British Lepidoptera*, Vol. v. but are very misleading, owing to no less than seven errors, four of which concern the colour of the parents of the families recorded. The following tables have been compiled from the original records of Harris, and of Hamling.

Bred by	Type × Type.					
	Imagines					
	Melanic			Type		
	Male	Female	Totals	Male	Female	Totals
T. H. Hamling (1904)	—	1	1	12	6	18
E. Harris (1905) ...	—	—	—	9	9	18
H. Onslow (1919) ...	—	—	—	3	—	3
Totals	1			39

¹ Pearce, W. G., *Ent. Rec.* Vol. x. p. 121, 1898.

² Southey, W. A., *Ent. Rec.* Vol. x. p. 122, 1898.

Melanic × *Melanic*.

Bred by	Imagines					
	Melanic			Type		
	Male	Female	Totals	Male	Female	Totals
E. Harris (1905) ...	34	34	68	—	—	—
G. Porritt (1905) ¹ ...	?	?	20	—	—	—
H. Onslow (1917) ...	3	1	4	—	—	—
Total	92			

Melanic (heterozygous for type) × *Melanic* (heterozygous for type).

Bred by	Imagines					
	Melanic			Type		
	Male	Female	Totals	Male	Female	Totals
T. H. Hamling (1904)	31	17	48	10	7	17
E. Harris (1905) ...	?	?	39	?	?	18
Totals	87 (71%)			35 (29%)
Expectation	91.5			30.5

Melanic (heterozygous for type) × *Type*.

Bred by		Imagines					
		Melanic			Type		
		Male	Female	Totals	Male	Female	Totals
W. G. Pearce (1895) ²	Female × Male	?	?	3	?	?	4
T. H. Hamling (1904)	Melanic × Type	7	4	11	7	2	9
T. H. Hamling (1904)	Type × Melanic	4	4	8	7	1	8
E. Harris (1904) ...	Melanic × Type	5	4	9	6	5	11
E. Harris (1905) ...	Melanic × Type	19	15	34	7	8	15
E. Harris (1905) ...	Type × Melanic	8	16	24	3	3	6
Totals	89 (63%)			53 (37%)
Expectation	71			71

It will be observed from these tables that in matings of type × type, with a single exception which is probably an error, nothing but type is given, and similarly, in matings of melanic × melanic, when one parent is homozygous, nothing but melanic is given.

In the families bred from melanic parents, both of which are heterozygous for type, the ratio of melanic to type insects is very nearly 3 : 1, as would be expected if melanism were dominant.

When a heterozygous melanic is crossed with a type insect, the ratio of type to melanic should be one of equality, but as will be seen from the figures in the last table, which includes crosses made both ways, i.e. the

¹ Porritt, G. See J. W. Tutt, *British Lepidoptera*, Vol. v. p. 59.

Pearce, W. G., *loc. cit.* (see p. 294).

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female being sometimes melanic and sometimes type, the ratio is very far from the expectation. In fact, there are 63 % of melanic instead of 50 %, which is rather closer to a ratio of 3 : 1 than to equality. In order to find out what the significance of this unusual ratio might be, a number of matings were made, the offspring from which are recorded in the following table :

Melanic (heterozygous for type) \times *Type*.

First Broods.

Family	Female \times Male	Imagines					
		Melanic			Type		
		Male	Female	Totals	Male	Female	Totals
H. Onslow (1917)	Melanic \times Type	2	1	3	3	1	4
H. Onslow (1919)	Type \times Melanic	5	1	6	4	1	5
'19 A	" \times "	7	1	8	3	3	6
'19 B	" \times "	2	3	5	3	1	4
'20 aA	Melanic \times Type	9	5	14	4	6	10
'20 aB	" \times "	6	6	12	10	10	20
'20 aC	" \times "	2	5	7	2	2	4
'20 aD	Type \times Melanic	4	3	7	4	4	8
'20 aE	" \times "	4	5	9	6	4	10
'20 bF	" \times "	4	4	8	4	9	13
Totals	79 (48.5%)	84 (51.5%)		
Expectation	81.5	81.5		

In these experiments it seems clear that the factor for melanism behaves normally, producing as many black insects as type. As however the numbers were not very large, those insects which emerged in July 1920 were paired, so as to obtain eggs from which a second brood could be raised. This was accomplished and the numerous larvae were fed first on lilac and then on privet, but it happened that there was a very severe frost in December, which caused the leaves of all the privet shrubs to fall. For various reasons no attempt was made to give the larvae, which were nearly full grown, any other food, and less than half of them succeeded in spinning cocoons. Of these only about half pupated completely and they emerged in May 1921, about a month after those of the first broods, which had hibernated in the pupal state. The result of these matings is given in the table on p. 297.

A glance shows that although the numbers are very small, the ratio of melanic to type is different from that given by the first broods in the previous table, and in this the experiments resemble those of Hamling and of Harris. When it is remembered that the mortality in the second broods was over 75 %, the explanation of this difference between the first and second broods does not seem very far to seek. The inference is that the mortality was selective, more melanic insects being able to

Melanic (heterozygous for type) \times *Type*.

Second Broods.

Family	Female \times Male	Imagines					
		Melanic			Type		
		Male	Female	Totals	Male	Female	Totals
'20 <i>cM</i>	Melanic \times Type	6	2	8	1	2	3
'20 <i>cN</i>	Type \times Melanic	2	2	4	—	3	3
'20 <i>cO</i>	Melanic \times Type	3	6	9	3	2	5
'20 <i>cP</i>	Type \times Melanic	3	1	4	1	1	2
'20 <i>cQ</i>	" \times "	1	2	3	—	1	1
'20 <i>cR</i>	" \times "	—	1	1	—	—	—
'20 <i>cS</i>	" \times "	—	—	—	2	—	2
'20 <i>cT</i>	" \times "	1	—	1	—	—	—
'20 <i>cU</i>	" \times "	3	2	5	1	—	1
'20 <i>cV</i>	" \times "	1	—	1	—	—	—
'20 <i>cX</i>	" \times "	—	—	—	1	—	1
'20 <i>cY</i>	" \times "	1	—	1	1	—	1
Totals		37 (66 %)	19 (34 %)		
Expectation		28	28		

pupate successfully than type. That this was so, seemed to be indicated by the fact that several of the type insects were too weak to emerge and had to be assisted from their cocoons, whereas most of the melanic insects emerged normally. Whether this will also explain the excess of melanics obtained by Hamling and Harris is doubtful, especially as there is no record as to whether these insects belonged to the first or second broods. It does not seem improbable, however, that in their experiments there was a mortality which favoured the stronger melanic insects at the expense of the type. It should be mentioned that Southey¹ is not of this opinion, as in his experience the melanic larvae were the weaker.

If this explanation is correct it emphasises an important point which has been mentioned before², namely the fact that many melanic forms appear more robust and hardy than the corresponding type forms. It is obvious that if a constitutional hardness accompanies melanism, selection would very soon cause these forms to replace type insects in localities where the mutation has occurred. Other factors might assist in bringing this about, but they would probably be much less important. From this view less stress need be laid on the occurrence of melanic varieties in manufacturing districts, and the numerous black forms that have arisen in the rural districts of the south and elsewhere do not appear anomalous.

¹ Southey, *loc. cit.* (see p. 294).

² Onslow, H., *Journal of Genetics*, Vol. ix, No. 4, 1920.

CONCLUSIONS.

1. The observations of Hamling and Harris seemed to show that although the factor for melanism in *Hemerophila abruptaria* is dominant to that for the type form, yet the ratio of type to melanic is not always a simple Mendelian phenomenon.

2. Nevertheless, a repetition of their work shows a ratio of type to melanic in the first broods, very closely approaching the equality expected.

3. In another set of matings, which produced the second broods, the mortality for various reasons was over 75 %. In this case, as in the experiments of Hamling and Harris, the ratio was nearer 3 melanic to 1 type than equality. This suggests that there may have been a selective mortality in favour of the melanic insects, which disturbs the normal ratio.

4. That a certain constitutional strength seems to accompany many melanic forms has been pointed out by other authors, and attention is here drawn to the fact that this would account more easily than other hypothesis for the rapid replacement of type by melanic varieties.

In conclusion I have to thank the British Association for a grant of £25 which helped to defray the expenses of 1920-1, and Miss Helen Moodie for her help in the routine work. I am also indebted to Professor Punnett for reading the MS. of the paper.

DESCRIPTION OF PLATE XXVIII.

Hemerophila abruptaria and var. *fuscata*, Tutt. Natural size.

- 1, 2. *H. abruptaria*. Typical ♀ ♀.
- 3, 4. *H. abruptaria*. Dark ♀ ♀, showing the same depth of colour as the typical ♂.
- 5, 6. *H. abruptaria*. Typical ♂ ♂.
- 7, 8. Var. *fuscata*. Melanic ♀ ♀, in which the ground colour and that of the band on the fore wings are the same.
- 9, 10. Var. *fuscata*. Melanic ♂ ♂, the band in which is slightly lighter than the ground colour.
- 11, 12. Var. *fuscata*. Melanic ♂ ♂ from the second broods. These insects are smaller than those of the earlier broods, and the central area of the fore wings is somewhat paler.



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REMARKS ON THE METHOD OF CALCULATION¹ PROPOSED BY MR H. L. TRACHTENBERG FOR DIALLEL CROSSINGS.

BY KIRSTINE SMITH, D.Sc.

FROM a mathematical or statistical point of view it may be argued that an arbitrary assumption about the generative value of one of the parents is *formally* unsatisfactory, although one must admit, considering the nature of generative values, which have no natural zero point, that in *reality* it is of absolutely no consequence.

The remedy proposed by Mr Trachtenberg, however, seems to me worse than this slight lack of form. While professing to avoid an *arbitrary* assumption it appears that the author only replaces it by an *unmaintainable* assumption. He does not seem to notice that in supposing that the personal values of parents represent their generative values with the same degree of accuracy as that with which the generative value of a group of offspring is observed from a single of its individuals he really makes a new assumption and, as we shall see, a wrong assumption. To realise this we only need to look at Mr Trachtenberg's results comparing personal and generative values for parents and offspring, from which I have calculated the following differences and their squares:

Parents		Offspring	
$d_p = \text{pers.} - \text{gener.}$	d_p^2	$d_\sigma = \text{obs.} - \text{calc.}$	d_σ^2
- .22	.048	+ .03	.0009
- .25	.063	+ .05	.0025
+ .17	.029	- .05	.0025
- 1.44	2.074	.00	.0000
+ .76	.578	+ .01	.0001
+ .10	.010	- .03	.0009
- .28	.078	+ .01	.0001
		+ .01	.0001
Total...	2.88	+ .02	.0004
Mean value of d_p^2 : 0.411		- .06	.0036
		+ .03	.0009
		.00	.0000
		Total012
		Mean value of d_σ^2 : 0.0010	

¹ "The Analysis of the results of Professor Johannes Schmidt's diallel crossings with trout." By H. L. Trachtenberg, B.A., in *Journal of Genetics*, Vol. xi. No. 1, 1921, pp 75—78.

According to Mr Trachtenberg's supposition the squared standard deviation of a personal value of a parent is 50 times that of the mean for a group of offspring. Now we find here that deviations between observed and theoretical values are on an average more than 400 times as great for parents as for offspring. We must therefore conclude that the supposition is wrong and reject it.

This result ought to be emphasised because it is a fundamental part of the plan of the experiments with diallel crossings that the environmental conditions are kept uniform for all groups of offspring, while on the other hand, for all we know, the parents have developed in quite different environments. Hence there is no reason to expect that their personal values, apart from an unknown constant common to all of them, should coincide with their generative values to the same order of accuracy as we find they do for the offspring.

While thus the fundamental idea of Mr Trachtenberg's method of calculation is wrong it is only fair to admit that practically it does not give so bad results, because the 7 parental observations weigh very little as compared with the 12×50 observations of offspring.

The correct proceeding when introducing the personal values in the calculation is of course to give to each of them a weight of only $\frac{1}{400}$ of that of the means of a group of offspring. But then the ratio $\frac{1}{400}$ is somewhat uncertain and has to be determined empirically.

It has therefore been found preferable to carry out the calculation in two *tempi*. At first the generative values are calculated according to the method of least squares, fixing an arbitrary value for one of the parents, and secondly the arbitrary zero point of the generative values is determined so as to make the squared differences between generative and personal values a minimum. This method has been followed in some of Dr Johannes Schmidt's publications concerning diallel crossings with trout while in others the second part of the calculation has been omitted as really unessential.

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